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ON THE TAXONOMY OF THE INDIAN OCEAN LIZARDS OF THE *PHELSUMA MADAGASCARIENSIS* SPECIES GROUP (REPTILIA, GECKONIDAE)[1]

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(With a colour and a monochrome plate & two text-figures)

Introduction

The taxonomy and phylogeny of the *Phelsuma madagascariensis* species group still contain vexed problems due to the wide dispersal of these geckos in the Indian Ocean, to inadequate samples from many localities in Madagascar and the rather remote, far-flung islands and to a certain lack of in-depth study of the available specimens and photos. Earlier authors (Angel, Boettger, Boulenger, Loveridge) regarded the taxa of the species group as varieties of *Phelsuma madagascariensis*; Rendahl's paper constituted a major step forward, as he clarified the situation of the sibling species in the Seychelles, but his conclusions were fully accepted only in recent times. Cheke's paper on the taxonomy of the *Phelsuma* of the Seychelles (Cheke 1982) gives a full account of the research history, which will not be repeated here. While Cheke's approach is biogeographical (cf. Cheke in press), our aim is to discuss the phylogeny of the species group in view of supplementary findings.

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Material and Methods

This paper is based on a study of:

1) specimens and photos obtained by Mr. Humayun Abdulali on the Andaman Islands in 1976, by Mr. Anthony S. Cheke on the Seychelles in 1976, by Mrs. Eva Minuth and Dr. Walter Minuth in northwest Madagascar in 1977;

2) specimens and photos communicated by numerous contributors which are mentioned in the list of materials examined;
3) living specimens, partly collected on the above mentioned excursions, partly obtained from third collectors, partly bred by one of us (W. M.)

All alcohol specimens are listed under the serial number of the junior author's collection (BSRC) and are stored in this collection except those transferred to the British Museum (Natural History) BM (NH) as indicated.

BSRC Geck 7 SC
Majunga, Malagasy Rep.
leg. H. Meier; rec. J. H. Brown 15.8.1975
d. J. H. Brown 30.5.1976.

BSRC Geck 8 SC
Praslin Island, Seychelles
leg. H. Meier; rec. J. H. Brown 15.8.1975
d. J. H. Brown 15.2.1976

BSRC Geck 27 SC
Félicité or La Digue Island
leg. Anthony S. Cheke November 1976
d. Anthony S. Cheke 19.6.1977

BSRC Geck 28 SC BM (NH) 1980. 357
probably Félicité Island, Seychelles
leg. Anthony S. Cheke November 1976
d. Anthony S. Cheke 19.6.1977

BSRC Geck 29 SC BM (NH) 1980. 352
? North Island, Seychelles
leg. Anthony S. Cheke Nov. 1976
d. Anthony S. Cheke 19.6.1977

BSRC Geck 30 SC
Frigate or Silhouette Island, Seychelles
leg. Anthony S. Cheke Nov. 1976
d. Anthony S. Cheke 19.6.1977

BSRC Geck 31 SC
Frigate or Silhouette Island, Seychelles
leg. Anthony S. Cheke Nov. 1976
d. Anthony S. Cheke 19.6.1977

BSRC Geck 32 SC
? Silhouette Island, Seychelles
leg. Anthony S. Cheke November 1976
d. Anthony S. Cheke 19.6.1977

BSRC Geck 33 SC
Félicité Island, Seychelles
leg. Anthony S. Cheke 21.11.1976
d. Anthony S. Cheke 19.6.1977

BSRC Geck 35 SC
Beau Vallon, Mahé Island, Seychelles
leg. Anthony S. Cheke 14.11.1976
d. Anthony S. Cheke 19.6.1977

BSRC Geck 36 SC
Frigate Island, Seychelles
leg. Anthony S. Cheke 8.11.1976
d. Anthony S. Cheke 19.6.1977

BSRC Geck 38 SC BM (NH) 1980. 355
Beau Vallon, Mahé Island, Seychelles
leg. Anthony S. Cheke 14.11.1976
d. Anthony S. Cheke 19.6.1977

BSRC Geck 40 SC BM (NH) 1980. 353
Frigate Island, Seychelles
leg. Anthony S. Cheke 8.11.1976
d. Anthony S. Cheke 19.6.1977

BSRC Geck 41 SC
Frigate Island, Seychelles
leg. Anthony S. Cheke 8.11.1976
d. Anthony S. Cheke 19.6.1977

BSRC Geck 42 SC
Anna La Passe, Silhouette Island, Seychelles
leg. Anthony S. Cheke 5.11.1976
d. Anthony S. Cheke 19.6.1977

BSRC Geck 43 SC
La Digue Island, Seychelles
leg. Anthony S. Cheke 19.11.1976
d. Anthony S. Cheke 19.6.1977

BSRC Geck 44 SC
La Digue Island, Seychelles
leg. Anthony S. Cheke 19.11.1976
d. Anthony S. Cheke 19.6.1977

BSRC Geck 45 SC BM (NH) 1979. 489
Félicité Island, Seychelles
leg. Anthony S. Cheke 21.11.1976
d. Anthony S. Cheke 19.6.1977

BSRC Geck 46 SC BM (NH) 1980. 358
La Digue Island, Seychelles

leg. Anthony S. Cheke 19.11.1976
d. Anthony S. Cheke 19.6.1977

BSRC Geck 47 SC BM (NH) 1980. 356
probably Félicité Island, Seychelles
leg. Anthony S. Cheke Nov. 1976
d. Anthony S. Cheke 19.6.1977

BSRC Geck 48 SC
most probably Beau Vallon, Mahé Island, Seychelles
leg. Anthony S. Cheke Nov. 1976
d. Anthony S. Cheke 19.6.1977

BSRC Geck 49 SC
North Island, Silhouette Island or Frigate Island, Seychelles
leg. Anthony S. Cheke Nov. 1976
d. Anthony S. Cheke 19.6.1977

BSRC Geck 50 SC
North Island, Silhouette Island or Frigate Island, Seychelles
leg. Anthony S. Cheke Nov. 1976
d. Anthony S. Cheke 19.6.1977

BSRC Geck 51 SC
North Island, Silhouette Island or Frigate Island, Seychelles
leg. Anthony S. Cheke Nov. 1976
d. Anthony S. Cheke 19.6.1977

BSRC Geck 68 SC
Menai, Cosmoledo Atoll, Indian Ocean
leg. P. Niedzwiedski October 1977
d. Anthony S. Cheke 7.9.1980

BSRC Geck 69 SC
Menai, Cosmoledo Atoll, Indian Ocean
leg. P. Niedzwiedski October 1977
d. Anthony S. Cheke 7.9.1980.

BSRC Geck 70 SC
Mahé, Seychelles
leg. U. Hoesch April 1981
d. W. Minuth July 1981

BSRC Geck 71 SC
La Digue, Seychelles
leg. U. Hoesch April 1981
d. W. Minuth July 1981

BSRC Geck 72 SC
La Digue, Seychelles
leg. U. Hoesch April 1981
d. W. Minuth July 1981

BSRC Geck 73 SC
La Digue, Seychelles
leg. U. Hoesch April 1981
d. W. Minuth July 1981

BSRC Geck 74 SC
La Digue, Seychelles
leg. U. Hoesch April 1981
d. W. Minuth July 1981

BSRC Geck 80 SC
Befotaka, Madagascar
leg. W. & E. Minuth August 1977
d. W. Minuth July 1981

BSRC Geck 81 SC
Befotaka, Madagascar
leg. W. & E. Minuth August 1977
d. W. Minuth July 1981

BSRC Geck 82 SC
Befotaka, Madagascar
leg. W. & E. Minuth August 1977
d. W. Minuth July 1981

BSRC Geck 8 MC
no locality
leg. W. Minuth; rec. J. H. Brown 15.8.1975
d. J. H. Brown 21.5.1976

BSRC Geck 13 MC
no locality
d. J. H. Brown 30.5.1976

BSRC Geck 20 MC
close vicinity of Diégo Suarez, Malagasy Republic
leg. H. Meier
d. J. H. Brown 30.5.1976

BSRC Geck 33 MC
close vicinity of Diégo Suarez, Malagasy Republic
leg. H. Meier; rec. J. H. Brown 2.4.76-19.10.76
d. J. H. Brown 28.4.1977

BSRC Geck 36 MC
Diégo Suarez, Malagasy Republic
leg. H. Meier; rec. André Brunke
d. J. H. Brown 28.4.1977

BSRC Geck 43 MC BM (NH) 1980. 351
Seychelles
leg. Anthony S. Cheke Nov. 1976
d. Anthony S. Cheke 19.6.1977

BSRC Geck 44 MC
could be Frigate or Silhouette Island

	Seychelles leg. Anthony S. Cheke Nov. 1976 d. Anthony S. Cheke 19.6.1977
BSRC Geck 45	MC ? Mahé Island, Seychelles leg. Anthony S. Cheke Nov. 1976 d. Anthony S. Cheke 19.6.1977
BSRC Geck 53	MC no locality leg. Rolf Heckhoff 2.4.1979 d. W. Frank 23.6.1977
BSRC Geck 55	MC no locality d. G. Terstappen 22.9.1979
BSRC Geck 56	MC no locality d. W. Frank 23.6.1977

The data for the morphometric tables have been double-checked to prevent errors. Abbreviations in the morphometric tables are the following :

specimen	—	gives collection number;
SVL	—	snout-vent-length, calipered to the nearest millimeter;
TL	—	tail-length, calipered to the nearest millimeter;
LH	—	length of head from the tip of the snout to the distal edge of the ear opening;
RE	—	length from rostral to eye, i.e. from the tip of the snout to the distal edge of the eye (eye-ring included);
NE	—	length from the nostril to the distal edge of the eye (eye-ring included);
WH	—	width of head, calipered in the widest point of the head by gently pressing the calipers to the sides of the head (scales and skull);
HH	—	height of head, calipered in the widest point of the head by gently pressing the calipers to the sides of the head (scales and skull);
H	—	average head granules situated on the snout (nearer to the rostral than to the eyes, upper side of head);
N	—	nuchal granules close to the occiput near the vertebral line;
D	—	average dorsal granules 1-2 mm right or left of the vertebral line near middorsum;
L	—	average lateral granules in the very center of the flanks (equidistant from dorsals and laterals and from fore and hind legs);
V	—	average ventral scales of the midventer;
G	—	average gular scales equidistant from a line combining the jaw angles and the ventral scales (ventral neck);
labials	—	all labials and enlarged granules bordering the mouth;
lamellae	—	all transversally enlarged scales and all scale rows under the complete rigit;
scansors	—	all lamellae with adhesive function including a distal terminal lamella and excluding a basal non-adhesive lamella which is set off a little bit from the adhesive pad;
preanal pores	—	all scales with pores and distinct scutes (= p., mainly in females).

Phelsuma of Malagasy and the Indian Ocean islands

1. **Phelsuma andamanensis**

BSRC Geck 12-14 SC

This species is known only from Port Blair, Andaman Islands, where our three specimens were also collected. This form being the only representative in the eastern Indian Ocean occurs far away from the main distribution of the genus, which is restricted to Malagasy and the western Indian Ocean islands. No *Phelsuma* has been found on the central Indian Ocean islands (Lakkadive and Maldive Islands, Sri Lanka) or on the Chagos Archipelago so that there is a considerable gap in the distribution of the genus which indicates a strong chance that *Phelsuma andamanensis* was accidentally transported to the Andaman Islands.

The morphometric data of our three specimens are given in table 1. The species is characterized by the absence of enlarged postmental scales and the following pattern: Dorsally light green. A red stripe (1 mm wide) from the nostril through the eye to the ear and there is a pre- and interocular red Λ-figure whose tip is in the first third of the snout; there are various spots on the rear of the head, which usually tend to extend trans-

TABLE 1

Phelsuma andamanensis, PORT BLAIR

Specimen	BSRC Geck	12 SC	13 SC	14 SC	Variation
sex		♂	♂	♂	
SVL		56	48	42	42 –56
TL		61	"59"	59	59 –61
SVL / TL		1.09	–	1.40	1.09– 1.40
LH		14.3	13.5	13.6	13.5 –14.3
RE		8.1	7.8	7.2	7.2 – 8.1
NE		6.5	6.6	6.3	6.3 – 6.6
WH		9.7	9.0	8.5	8.5 – 9.7
HH		5.9	6.3	6.0	5.9 – 6.3
LH/RE		1.76	1.73	1.89	1.73– 1.89
LH/NE		2.20	2.04	2.15	2.04– 2.15
LH/WH		1.47	1.50	1.6	1.47– 1.6
LH/HH		2.42	2.14	2.27	2.14– 2.42
WH/HH		1.64	1.42	1.42	1.42– 1.64
NE/HH		1.10	1.05	1.05	1.05– 1.10
gran.: II		0.4	0.3	0.3	0.3 – 0.4
N		0.15	0.1	0.1	0.1 – 0.15
D		0.2	0.25	0.2	0.2 – 0.25
L		0.5	0.25	0.2	0.2 – 0.5
V		0.7	0.55	0.5	0.5 – 0.7
G		0.35	0.1	0.1	0.1 – 0.35
L/D		2.5	1	1	1 – 2.5
H.1000/SVL		7.14	6.25	7.14	6.25– 7.14
N.1000/SVL		2.69	2.08	2.38	2.08– 2.69
D.1000/SVL		3.57	5.21	4.76	3.57– 5.21
L.1000/SVL		8.93	5.21	4.76	4.76– 8.93
V.1000/SVL		12.5	11.46	11.90	11.46–12.5
G.1000/SVL		6.25	2.08	2.38	2.08– 6.25
scales around midbody		80	88	90	80 –90
supralabials r/l		11/9	10	10/9	9 –11
sublabials r/l		9/8	10/9	9/8	8 –10
lamellae 4th toe		21	24	23	21 –24
scansors 4th toe		10	15	13	10 –15
lamellae 4th finger		18	20	22	18 –22
scansors 4th finger		10	11	14	10 –14
preanal pores r/l		15/16	14/15	14/13	13 –16

versally. Three red longitudinal bands (0.6-1.0 mm wide) are prominent on the nape, and there may be another two lateral rows of red spots or lines, one on each side of the neck. The anterior and mid-dorsum lack spots. The posterior dorsum and sacrum have irregular red spots (-2.0 mm ϕ), which tend to enlarge and fuse transversally. Underneath, the geckos are yellowish and whitish at least on the throat and the anal and femoral region.

The dorsal pattern is not always visible, and there may be true "concolor" — specimens; they occur in the same Port Blair population.

2. **Phelsuma longinsulae** ssp.

This complex has its center on the western group of the Seychelles, the Mahé group, and on Frigate; Cheke (1982, in press) lists the locality records for the Amirante Islands, from where we lack specimens.

Phelsuma longinsulae is a green *Neophelsuma* species with a reduced lateral pattern, a dark red stripe of 1.5 mm width from the nostril to the eye, a $\wedge$ -figure of -1.0 mm width on the snout, variable red postocular and on back of head spots, light (whitish or reddish) spots on the legs and (fading in adults) on the flanks, a longitudinal pattern of red spots (transversally fusing near sacrum). The morphometric data are given in tables 2 ff. It lacks keeled chest scales; and head is more pointed than in *P. sundbergi* (cf. Cheke, in press).

The type of this species has been collected on Long Island near the harbour of Victoria, Mahé. Cheke has already demonstrated that this typical form occurs on Frigate, too, and that this island may be the true center of distribution of this form, Long Island containing only a small, maybe even short-lived population secondarily transported there, probably by natives. Rendahl's taxon *pulchra* has its type locality on Mahé and his taxon *cousinense* from Cousine Island (near Mahé) is consi-

TABLE 2

DIAGNOSES OF THE SEYCHELLES *Phelsuma longinsulae*

Subspecies	*longinsulae*	*pulchra*	*umbrae*	*rubra*
Island	Frigate	Mahé	Silhouette	North
Specimens	36, 40, 41, 49, 51 SC	35, 38, 48, 70 SC	32, 42, 30 SC	29, 50 SC
Shape	moderate	moderate to robust	slender	slender
SVL	41 –51	49 –59	43 –55	43 –55
LH/RE	1.79- 1.87	1.77– 1.89	1.84– 1.91	1.88– 1.94
LH/WH	1.58– 1.62	1.49– 1.58	1.62– 1.72	1.67– 1.71
L/D	1 – 2.33	2 – 2.5	1.33– 1.5	1 – 2
H.1000/SVL	6.00– 8.77	8.16–10.01	7.27–11.11	6.98– 7.27
D.1000/SVL	2.88– 3.70	2.58– 4.08	4.0 – 5.45	3.64– 4.65
L.1000/SVL	3.66– 7.41	5.17– 9.62	4.65– 7.27	4.65– 7.27
V.1000/SVL	9.26–14.81	10.34–13.79	10.91–13.33	9.09– 9.30
G.1000/SVL	1.85– 2.78	2.73– 3.45	1.82– 2.33	2.33– 3.64
scales around midbody	78 –92	76 –88	76 –98	70 –76
supralabials	8 –11	9 –12	7 – 9	8 – 9
scansors 4th toe	10– 15	12 –14	11 –13	12
lamellae 4th finger	18 –22	21 –23	17 –18	18
scansors 4th finger	9 –13	12 –14	9 –10	10
preanal pores	10 –15	8 –16	6 – 9	—

TABLE 2 (Contd.)

Subspecies	*longinsulae*	*pulchra*	*umbrae*	*rubra*
dorsal ground colour	bright green, sometimes a yellowish cast	dull green, rarely yellowish, sometimes bluish	bright green, sometimes a yellowish cast	bright green
dorsal markings a) colour	dull red	dull red	bright red	bright red
b) pattern posterior dorsum	markings prominent (—2 mm ϕ) and tending to fuse transversally near sacrum	markings prominent (—2 mm ϕ) and tending to fuse transversally near sacrum	many small red markings may coalesc transversally near sacrum, but always not as crudely and conspicuously as in specimens from Mahé or Frigate; markings sometimes form three longitudinal irregular lines; markings fade anteriorly like Frigate	large rounded spots (—1.5 mm ϕ) tending to coalesc longitudinally in three (near sacrum even four longitudinal stripes, which continue throughout the dorsum and may fuse transversally near sacrum
middle and anterior dorsum	markings usually arranged in three poorly defined longitudinal lines; markings fade anteriorly	markings (—1 mm ϕ) definitely in three longitudinal lines; markings fade anteriorly like Frigate		
Ratio: Ground colour/pattern	red pattern may take 50% of posterior and middle dorsum; almost no pattern anteriorly			red pattern takes most space of total dorsum (50% +)
Flanks (adult specimens)	most white spots fade, leaving a mottling of (whitish or red) and dark greenish (undefined) spots	a) well defined white spots which anteriorly form parallel transversal bars, or b) irregular red brown spots	at least some usually well defined whitish spots, almost like ocelli	like Silhouette

TABLE 3A

Phelsuma longinsulae longinsulae, FRIGATE

Specimen	BSRC Geck	36 SC	40 SC	41 SC	Variation
Sex		♀	♂	♂?	
SVL		54	52	41	41 –54
TL		"54"	60	"54"	60
SVL / TL		–	1.15	–	1.15
LH		13.0	13.1	11.0	11.0 –13.1
RE		7.0	7.0	6.0	6.0 – 7.0
NE		5.5	6.4	4.7	4.7 – 6.4
WH		8.1	8.3	6.8	6.8 – 8.3
HH		5.0	5.9	4.4	4.4 – 5.9
LH/RE		1.86	1.87	1.83	1.83– 1.87
LH/NE		2.36	2.05	2.34	2.05– 2.36
LH/WH		1.60	1.58	1.62	1.58– 1.62
LH/HH		2.6	2.22	2.5	2.22– 2.6
WH/HH		1.62	1.41	1.55	1.41– 1.62
NE/HH		1.1	1.08	1.07	1.07– 1.1
gran.: H		0.4	0.4	0.3	0.3 – 0.4
N		0.1	0.15	0.1	0.1 – 0.15
D		0.2	0.15	0.15	0.1 – 0.2
L		0.4	0.35	0.15	0.15– 0.4
V		0.5	0.6	0.4	0.4 – 0.6
G		0.1	0.1	0.1	0.1
L/D		2	2.33	1	1 – 2.33
H.1000/SVL		7.41	7.69	7.32	7.32– 7.69
N.1000/SVL		1.85	2.88	2.44	1.85– 2.88
D.1000/SVL		3.70	2.88	3.66	2.88– 3.70
L.1000/SVL		7.41	5.73	3.66	3.66– 7.41
V.1000/SVL		9.26	11.54	9.76	9.26–11.54
G.1000/SVL		1.85	1.92	2.44	1.85– 2.44
scales around midbody		92	80	88	80 –92
supralabials r/l		11/10	10/9	8/10	8 –11
sublabials r/l		9	6/7	7	7 – 9
lamellae 4th toe		26	20	22	20 –26
scansors 4th toe		13	10	13	10 –13
lamellae 4th finger		–	18	20	18 –20
scansors 4th finger		–	9	12	9 –12
preanal pores r/l		15/15	12/10	12/11 p	10 –15/

dered to be a synonym. So far we follow Cheke's opinion. In order to determine the subspecific variation of *Phelsuma longinsulae*, the junior author has drawn up a detailed description of each specimen (cf. tables 3-7 for morphometric data). The specimens with a definite locality were then lumped together so that a variation was determined. The data for the morphometric variation in the four islands Frigate, Mahé, Silhouette and North —

TABLE 3B

Phelsuma longinsulae longinsulae

Specimen	BSRC Geck	49 SC	51 SC	Total variation of subspecies
sex		♂	♂	
SVL		57	54	41 –57
TL		"59"	"52"	60
SVL/TL		–	–	1.15
LH		14.0	12.0	11.0 –14.0
RE		7.7	6.7	6.0 – 7.7
NE		6.5	5.6	4.7 – 6.5
WH		8.8	7.5	6.8 – 8.8
HH		6.0	5.5	4.4 – 6.0
LH/RE		1.82	1.79	1.79– 1.87
LH/NE		2.15	2.14	2.0 – 2.36
LH/WH		1.59	1.6	1.58– 1.62
LH/HH		2.33	2.18	2.18– 2.6
WH/HH		1.47	1.36	1.36– 1.62
NE/HH		1.08	1.02	1.02– 1.1
gran.: H		0.5	0.4	0.3 – 0.5
N		0.2	0.1	0.1 – 0.2
D		0.2	0.2	0.1 – 0.2
L		0.25	0.3	0.15– 0.4
V		0.6	0.8	0.4 – 0.8
G		0.1	0.15	0.1 – 0.15
L/D		1.25	1.5	1 – 2.33
H.1000/SVL		8.77	7.41	6.0 – 8.77
N.1000/SVL		3.51	1.85	1.85– 3.51
D.1000/SVL		3.51	3.70	2.88– 3.70
L.1000/SVL		4.39	5.56	3.66– 7.41
V.1000/SVL		10.53	14.81	9.26–14.81
G.1000/SVL		1.75	2.78	1.75– 2.78
scales around midbody		78	86	78 –92
supralabials r/l		8/9	9	8 –11
sublabials r/l		9/8	7/8	7 – 9
lamellae 4th toe		25	25	20 –26
scansors 4th toe		15	13	10 –15
lamellae 4th finger		21	22	18 –22
scansors 4th finger		10	13	9 –13
preanal pores r/l		14/12 p	13/13 P	10 –15/

as derived from these specimens (including males and females for all islands except North Island) — are given in a synoptic table (table 9). Then it was determined, into which variation each of the morphometric and pattern data of a given specimen without exact locality data fitted. As the basic variation data were derived from males and females (except those for North Island), a comparison of the uncertain specimen with a specimen of the same sex regularly shows even clearer results of affinity. The process of assessing the speci-

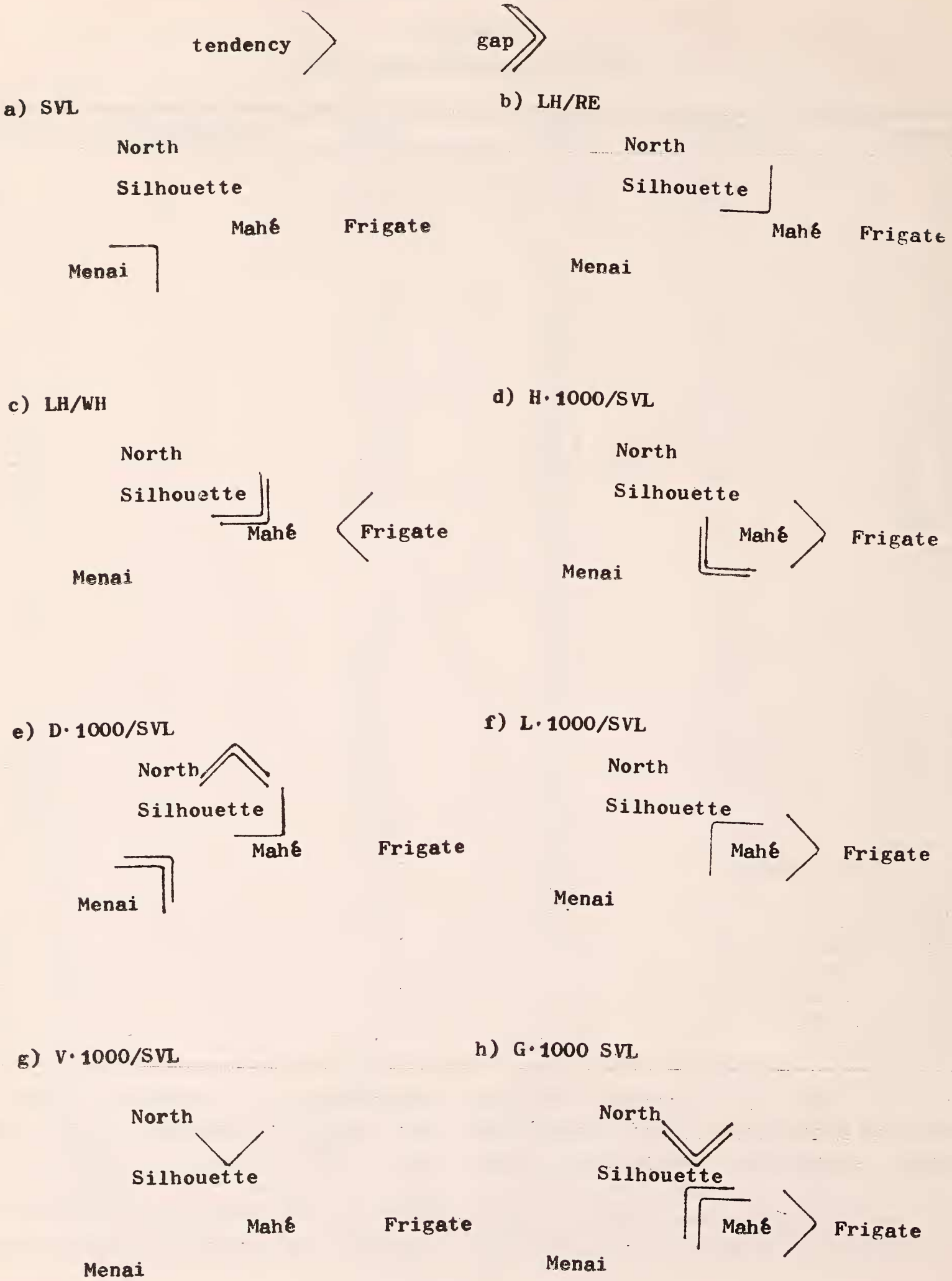


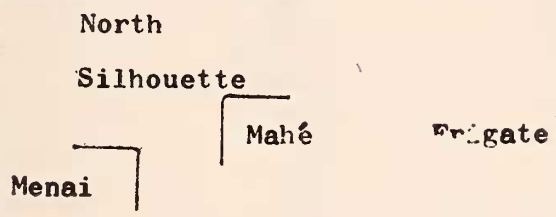
Fig. 1. Character divergence in *Phelsuma longinsulae.*

FIGURE. 1

i) L/D

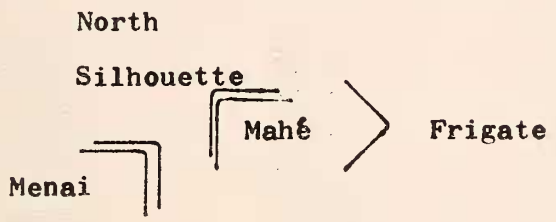
j) scales around midbody

k) labials (supralabials)



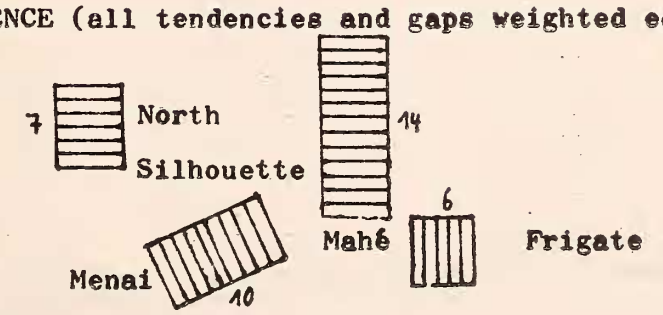
l) (lamellae and) scansors 4th toe

m) lamellae and scansors 4th finger



n) preanal pores

TOTAL MORPHOMETRIC DIVERGENCE (all tendencies and gaps weighted equally)



Affinities in gestalt and pattern

Fig. 1 (contd.)

TABLE 4

Phelsuma longinsulae pulchra, MAHE

Specimen BSRC Geck	35 SC	38 SC	48 SC	70 SC	Variation
sex	♀	♀	♂	♂	
SVL	5.8	5.9	5.5	4.9	4.9 – 5.9
TL	"6.0"	"5.9"	"3.6"	"5.6"	–
SVL/TL	–	–	–	–	–
LH	14.8	14.0	14.0	12.6	12.6 –14.8
RE	8.0	7.9	7.4	6.8	6.8 – 8.0
NE	6.3	6.4	6.1	5.4	5.4 – 6.3
WH	9.6	9.4	9.0	8.0	8.0 – 9.6
HH	6.2	6.4	6.3	5.0	5.0 – 6.4
LH/RE	1.85	1.77	1.89	1.88	1.77– 1.89
LH/NE	2.35	2.19	2.29	2.33	2.19– 2.35
LH/WH	1.54	1.49	1.56	1.575	1.49– 1.58
LH/HH	2.39	2.19	2.22	2.52	2.19– 2.52
WH/HH	1.55	1.47	1.43	1.6	1.43– 1.6
NE/HH	1.02	1	0.97	1.08	0.97– 1.08
gran.: H	0.5	0.5	0.55	0.4	0.4 – 0.55
N	0.1	0.2	0.2	0.1	0.1 – 0.2
D	0.15	0.2	0.2	0.2	0.15– 0.2
L	0.3	0.5	0.5	0.4	0.3 – 0.5
V	0.6	0.8	0.7	0.6	0.6 – 0.8
G	0.2	0.2	0.15	0.15	0.15– 0.2
L/D	2	2.5	2.5	2	2 – 2.5
H.1000/SVL	8.62	9.62	10.01	8.16	8.16–10.01
N.1000/SVL	1.72	3.45	3.64	2.04	1.72– 3.64
D.1000/SVL	2.58	3.45	3.64	4.08	2.58– 4.08
L.1000/SVL	5.17	9.62	9.09	8.16	5.17– 9.62
V.1000/SVL	10.34	13.79	12.73	12.24	10.34–13.79
G.1000/SVL	3.45	3.45	2.73	3.06	2.73– 3.45
scales around midbody	88	76	80	84	76 –88
supralabials r/l	11/12	10/11	9/11	10	9 –12
sublabials r/l	8	9	7	7/8	7 – 9
lamellae 4th toe	28	22	22	24	22 –28
scansors 4th toe	13	14	12	13	12 –14
lamellae 4th finger	23	22	23	21	21 –23
scansors 4th finger	12	12	14	12	12 –14
preanal pores r/l	some p	8/8 p	14/14 p	16/16	8 –16/

mens of uncertain origin is shown in table 10; some specimens could not be assigned to any one population, and consequently their data were included in the total specific variation only. The data of the specimens which were assessed with certainty are included in a second synoptic table giving the variation data for the different islands. Based on this inductive

TABLE 5

Phelsuma longinsulae umbrae

Specimen	BSRC Geck	Silhouette 32 SC	Sihouette 42 SC	Frigate or Sihouette 30 SC	Variation
sex		♀	♂	♀	–
SVL		50	45	55	45 –55
TL		"20"	59	"79"	59
SVL/TL		–	1.31	–	1.31
LH		12.4	12.0	12.9	12.0 –12.9
RE		6.5	6.4	7.0	6.4 – 7.0
NE		5.1	5.5	5.6	5.1 – 5.6
WH		7.5	7.4	7.5	7.4 – 7.5
HH		5.0	5.0	5.4	5.0 – 5.4
LH/RE		1.91	1.87	1.84	1.84– 1.91
LH/NE		2.43	2.18	2.30	2.18– 2.43
LH/WH		1.65	1.62	1.72	1.62– 1.72
LH/HH		2.48	2.40	2.39	2.39– 2.48
WH/HH		1.5	1.48	1.39	1.39– 1.5
NE/HH		1.02	1.1	1.04	1.02– 1.1
gran.: H		0.4	0.5	0.4	0.4 – 0.5
N		0.1	0.1	0.2	0.1 – 0.2
D		0.2	0.2	0.3	0.2 – 0.3
L		0.3	0.3	0.4	0.3 – 0.4
V		0.6	0.6	0.6	0.6
G		0.1	0.1	0.1	0.1
L/D		1.5	1.5	1.33	1.33– 1.5
H.1000/SVL		8.0	11.11	7.27	7.27–11.11
N.1000/SVL		2.0	2.22	3.64	2.0 – 3.64
D.1000/SVL		4.0	4.44	5.45	4.0 – 5.45
L.1000/SVL		6.0	6.66	7.27	6.0 – 7.27
V.1000/SVL		12.0	13.33	10.91	10.91–13.33
G.1000/SVL		2.0	2.22	1.82	1.82– 2.22
scales around midbody		76	90	98	76 –98
supralabials r/l		9/8	9/7	9/8	7 – 9
sublabials r/l		8	8/7	7/8	7 – 8
lamellae 4th toe		21	23	24	21 –24
scansors 4th toe		11	13	12	11 –13
lamellae 4th finger		17	18	18	17 –18
scansors 4th finger		10	9	10	9 –10
preanal pores r/l		9/8	8/6	–	6 – 9

method, we got the results listed in table 11 and accordingly recognize four subspecies in the Seychelles:

Phelsuma longinsulae longinsulae
Frigate; tt : Long Island nr. Mahé
BSRC Geck 36, 40, 41, 49, 51 SC

TABLE 6

Phelsuma longinsulae rubra

specimen	BSRC Geck	North 29 SC	North, Frigate or Silhouette 50 SC	variation
Sex		♂	♀	—
SVL		55	43	43 — 55
TL		64	"58"	64
SVL/TL		1.16	—	1.16
LH		13.4	11.3	11.3 — 13.4
RE		6.9	6.0	6.0 — 6.9
NE		5.5	4.7	4.7 — 5.5
WH		8.0	6.6	6.6 — 8.0
HH		5.5	4.6	4.6 — 5.5
LH/RE		1.94	1.88	1.88 — 1.94
LH/NE		2.44	2.40	2.40 — 2.44
LH/WH		1.67	1.71	1.67 — 1.71
LH/HH		2.44	2.46	2.44 — 2.46
WH/HH		1.45	1.43	1.43 — 1.45
NE/HH		1	1.02	1 — 1.02
gran.: H		0.4	0.3	0.3 — 0.4
N		0.1	0.1	0.1
D		0.2	0.2	0.2
L		0.4	0.2	0.2 — 0.4
V		0.5	0.4	0.4 — 0.5
G		0.2	0.1	0.1 — 0.2
L/D		2	1	1 — 2
H.1000/SVL		7.27	6.98	6.98 — 7.27
N.1000/SVL		1.82	2.33	1.82 — 2.33
D.1000/SVL		3.64	4.65	3.64 — 4.65
L.1000/SVL		7.27	4.65	4.65 — 7.27
V.1000/SVL		9.09	9.30	9.09 — 9.30
G.1000/SVL		3.64	2.33	2.33 — 3.64
scales around midbody		70	76	70 — 76
supralabials r/l		8/9	—/8	8 — 9
sublabials r/l		8	7	7 — 8
lamellae 4th toe		—	24	24
scansors 4th toe		—	12	12
lamellae 4th finger		—	18	18
scansors 4th finger		—	10	10
preanal pores r/l		—	—	—

Phelsuma longinsulae pulchra
Mahé, Cousine; tt: Mahé;
Cousin for *cousinense* Rendahl
BSRC Geck 35, 38, 48, 70 SC

Phelsuma longinsulae umbrae, ssp. nov.
tt : Silhouette (d.n.)
Holotype : BSRC Geck 42 SC
Paratypes : BSRC Geck 32, 30 SC

TABLE 7

Phelsuma longinsulae SSPP. (EXCL. *menaiensis*)

Specimen	BSRC Geck	*longinsulae* or *pulchra* 45 MC	*longinsulae* or *pulchra* 31 SC	*longinsulae* or *umbrae* 44 MC	Seychelles 43 MC
sex		♂	♀	♂	♂
SVL		55	56	50	54
TL		63	"50"	"55"	—
SVL/TL		1.15	—	—	—
LH		13.6	13.0	13.0	—
RE		7.7	6.8	7.0	—
NE		6.4	5.8	5.7	—
WH		9.5	8.0	7.8	—
HH		5.8	5.6	5.8	—
LH/RE		1.77	1.91	1.86	—
LH/NE		2.12	2.24	2.28	—
LH/WH		1.43	1.63	1.7	—
LH/HH		2.34	2.32	2.24	—
WH/HH		1.64	1.43	1.34	—
NE/HH		1.10	1.04	0.98	—
gran.: H		0.3	0.4	0.3	0.3
N		0.1	0.1	0.1	0.1
D		0.2	0.2	0.2	0.1
L		0.2	0.1–0.4	0.2	0.3
V		0.4	0.8	0.5	0.7
G		0.1	0.1	0.1	0.1
L/D		1	0.5–2.0	2	1.5
H.1000/SVL		5.45	7.14	6.00	5.6
N.1000/SVL		1.82	1.79	2.00	1.85
D.1000/SVL		3.63	3.57	2.00	3.7
L.1000/SVL		3.63	1.79–7.14	4.00	5.6
V.1000/SVL		7.27	14.29	10.00	12.96
G.1000/SVL		1.82	1.79	2.00	1.85
scales around midbody		80	80	90	82
supralabials r/l		10	10/9	11/10	—
sublabials r/l		8	8/7	8/7	—
lamellae 4th toe		30	30	20	21
scansors 4th toe		18	16	11	12
lamellae 4th finger		21	21	17	—
scansors 4th finger		12	11	9	—
preanal pores r/l		13/12	14/14	14/13	p

Phelsuma longinsulae rubra, ssp. nov.

tt : North Island

(d.n.: the name hints at the conspicuous pattern)

Holotype : BSRC Geck 29 SC

Paratype : BSRC Geck 50 SC

The types are described morphometrically in tables 5 and 6. Diagnoses are given in table 2.

3. **Phelsuma longinsulae menaiensis**

BSRC Geck 68, 69 SC

Cheke (1982) has placed the green *Neophelsuma* from Menai, Cosmoledo Atoll, in the

TABLE 8

Phelsuma longinsulae menaiensis, MENAI

Specimen BSRC Geck	68 SC	69 SC	Variation
sex	♀, 2 eggs	♂	
SVL	5.8	6.1	5.8 — 6.1
TL	"5.6"	"7.6"	—
SVL/TL	—	—	—
LH	14.7	15.4	14.7 — 15.4
RE	8.0	8.5	8.0 — 8.5
NE	6.4	7.4	6.4 — 7.4
WH	9.0	11.0	9.0 — 11.0
HH	6.0	8.3	6.0 — 8.3
LH/RE	1.81	1.81	1.81
LH/NE	2.27	2.08	2.08 — 2.27
LH/WH	1.61	1.4	1.4 — 1.61
LH/HH	2.42	1.86	1.86 — 2.42
WH/HH	1.5	1.325	1.325— 1.5
NE/HH	1.33	0.89	0.89 — 1.33
gran.: H	0.2	0.4	0.2 — 0.4
N	0.1	0.15	0.1 — 0.15
D	0.3	0.3	0.3
L	0.4	0.6	0.4 — 0.6
V	0.8	0.7	0.7 — 0.8
G	0.15	0.2	0.15 — 0.2
L/D	1.33	2	1.33 — 2
H.1000/SVL	3.44	5.56	3.44 — 5.56
N.1000/SVL	1.72	2.46	1.72 — 2.46
D.1000/SVL	5.17	4.92	4.92 — 5.17
L.1000/SVL	6.89	9.84	6.89 — 9.84
V.1000/SVL	13.79	11.48	11.48 — 13.79
G.1000/SVL	2.58	3.28	2.58 — 3.28
scales around midbody	90	88	88 — 90
supralabials r/l	9	8	8 — 9
sublabials r/l	7	8/7	7 — 8
lamellae 4th toe	21	22	21 — 22
scansors 4th toe	13	12	12 — 13
lamellae 4th finger	18	19	18 — 19
scansors 4th finger	11	11	11
preanal pores r/l	11–1–11	15/15	11 — 15/

species *longinsulae*. Indeed this form is hardly distinguishable from *Phelsuma longinsulae pulchra,* which occurs on Mahé. In shape it comes most closely to this lizard, as it is similarly robust. Its meristic data are given in table 8, from which a marked sexual dimorphism in head proportions is evident. In life it is dark green with dull red dorsal markings (-1.6 mm wide) in three irregular longitudinal rows. Legs and flanks are irregularly mottled. The head shows a ∧ -figure, a dark red stripe from the nostril to the eye, and a spotted temple. Underneath the lizard is whitish, the only marks being a grey semi-circular band on the inframaxillary reaching to the ear and some dark gular spots which may form a second inner semi-circle.

4. **Phelsuma chekei,** sp. nov.
   BSRC Geck 36 MC (Holotype),
   20 MC, 33 SC (Paratypes)

These specimens have been purchased from Mr. H. Meier, who collected them in the close vicinity of Diégo Suarez (pers. comm.). We therefore design as *type locality*: vicinity of Diégo Suarez, northern tip of Madagascar; d.n.: The new species is named after Anthony Cheke, a long-time friend of ours.

Diagnosis: The diagnostic meristic data are summarized in table 20.

The new species is rather robust and stout in shape, comparable to the forms of Menai and Mahé on the one hand and to the even

TABLE 9

Phelsuma longinsulae, VARIATION OF SPECIMENS WITH CERTAIN LOCALITY DATA ONLY

taxon	*rubra* (1)	*umbrae* (2)	*pulchra* (4)	*longinsulae* (3)	*menaiensis* (2)
specimens BSRC Geck	29 SC	32, 42 SC	35, 38, 48, 70 SC	36, 40, 41 SC	68, 69 SC
SVL	55	45 –50	49 –59	41 –54	58 –61
SVL/TL	1.16	1.16– 1.51	—	1.15	—
LH/RE	1.94	1.87– 1.91	1.77– 1.89	1.83– 1.87	1.81
LH/NE	2.44	2.18– 2.43	2.19– 2.35	2.05– 2.36	2.08– 2.27
LH/WH	1.67	1.62– 1.65	1.49– 1.58	1.58– 1.62	1.4 – 1.61
LH/HH	2.44	2.40– 2.48	2.19– 2.52	2.22– 2.6	1.86– 2.42
WH/HH	1.45	1.48– 1.5	1.43– 1.6	1.41– 1.62	1.325–1.5
NE/HH	1	1.02– 1.1	0.97– 1.08	1.07– 1.1	0.89– 1.33
L/D	2	1.5	2 – 2.5	1 – 2.33	1.33– 2
H.1000/SVL	7.27	8.0 –11.11	8.16–10.01	7.32– 7.69	3.44– 5.56
N.1000/SVL	1.82	2.0 – 2.22	1.72– 3.64	1.85– 2.88	1.72– 2.46
D.1000/SVL	3.64	4.0 – 4.44	2.58– 4.08	1.92– 3.70	4.92– 5.17
L.1000/SVL	7.27	6.0 – 6.66	5.17– 5.62	3.66– 7.41	6.89– 9.84
V.1000/SVL	9.09	12.0 –13.33	10.34–13.79	9.26–11.54	11.48–13.79
G.1000/SVL	3.64	2.0 – 3.33	2.73– 3.45	1.85– 2.44	2.58– 3.28
scales around midbody	70	76 –90	76 –88	80 –92	88 –90
supralabials	8/9	7 – 9	9 –12	8 –11	8 – 9
sublabials	8	7 – 8	7 – 9	7 – 9	7 – 8
lamellae 4th toe	—	21 –23	22 –28	20 –26	21 –22
scansors 4th toe	—	11 –13	12 –14	10 –13	12 –13
lamellae 4th finger	—	17 –18	21 –23	18 –20	18 –19
scansors 4th finger	—	9 –10	12 –14	9 –12	11
preanal pores	—	6 – 9/	8 –16/	10 –15/	11 –15/

TABLE 10

Phelsuma longinsulae, AFFINITIES OF SPECIMENS WITHOUT CERTAIN LOCALITY DATA

specimen	S, F 30 SC	N, S, F 50 SC	N. S, F 49 SC	N, S, F 51 SC
A. SVL	N, S, M, F	N, S, M, F	nr. N, M, nr. F	N, M, F
B. LH/RE	nr. S, M, F	S, M, nr. F	M, nr. F	M, nr. F
LH/NE	S, M, F	S, nr. F	nr. S, nr. M, F	F
LH/WH	nr. S	nr. S	nr. S, nr. M, F	nr. S, M, F
LH/NH	nr. S, M, F	S, M, F	M, F	nr. M, nr. F
WH/HH	nr. M, nr. F	nr. S, M, F	nr. S, M, F	nr. F
NE/HH	S, M, nr. F	S, M, nr. F	S, M, F	nr. N, S, M, nr. F
C. L/D	nr. S, nr. F	nr. S, F	nr. S, F	S, nr. M, F
H.1000/SVL	N, nr. F	nr. N, nr. F	S, M	nr. N, F
N.1000/SVL	N, nr. F	nr. S, M, F	M	nr. N, nr. S, M, F
D.1000/SVL	nr. S	nr. S, M	nr. N, nr. S, M, F	nr. N, nr. S, M, F
L.1000/SVL	nr. S, M, F	M, F	F	nr. S, M, F
V.1000/SVL	M, F	nr. M, F	M, F	nr. M
G.1000/SVL	nr. F	S, nr. M, F	nr. F	S, M, nr. F
scales around midbody	nr. S, nr. F	S, M	S, M, nr. F	S, M, F
supralabials	S, M, F	S, nr. M, F	N, S, nr. M, F	S, M, F
sublabials	S, M, F	S, M, F	nr. N, nr. S, M, F	S, M, F
lamellae 4th toe	nr. S, M, F	nr. S, M, F	nr. S, M, F	nr. S, M, F
scansors 4th toe	S, M, F	S, M, F	nr. S, nr. M, nr. F	S, M, F
lamellae 4th finger	S, M, F	S, F	M, nr. F	M, nr. F
scansors 4th finger	S, F	S, F	S, nr. M, F	M, nr. F
preanal pores	—	—	M, F	M, F
D. pattern	S	N	F	F
E. Characters are in/near/to variation of				
North (only N)	3x	3x (1x)	4x	5x
Silhouette (only S)	17x (3x)	18x (1x)	13x	12x
Mahé (only M)	13x	15x	19x	19x (1x)
Frigate (only F)	19x (1x)	18x	21x (3x)	22x (3x)
F. Subspecific Classification (according to weighted character affinities and subjective impression)	*umbrae* (Silhouette)	*rubra* (North)	*longinsulae* (Frigate)	*longinsulae* (Frigate)

TABLE 10 (*Contd.*)

specimen	F, S 44 MC	F, S 31 SC	Mahé 45 MC	Seychelles 43 MC
A. SVL	N, S, M, F	nr. N, M, nr. F	N, M, F	N, M, F
B. LH/RE	nr. S, M, F	N, S, nr. M, nr. F	M, nr. F	—
LH/NE	S, M, F	S, M, F	F	—
LH/WH	nr. S	nr. N, S, nr. M, nr. F	nr. M	—
LH/NH	M, F	M, F	M, F	—
WH/HH	nr. F	nr. N, nr. S, M, F	nr. M, nr. F	—
NE/HH	nr. N, nr. S, M	S, M, nr. F	S, nr. M, F	—
C. L/D	nr. S, M, F	nr. S, nr. M, nr. F	nr. S, F	S, nr. M, F
H.1000/SVL	nr. F	nr. N, nr. F	to N, to F	to F
N.1000/SVL	nr. N, S, M, F	nr. N, nr. S, M, nr. F	N, nr. S, M, nr. F	nr. N, nr. S, M, F
D.1000/SVL	nr. M, F	nr. N, nr. S. M, F	N, nr. S, M, F	nr. N, nr. S, M, F
L.1000/SVL	F	nr. N, nr. S, M, F	nr. F	nr. S, M, F
V.1000/SVL	nr. M, F	M	to F	S, M
G.1000/SVL	S, F	nr. S, nr. F	nr. S, nr. F	nr. S, F
scales around midbody	S, nr. M, F	S, M, F	S, M, F	S, M, F
supralabials	M, F	nr. N, nr. S, M, F	M, F	—
sublabials	N, S, M, F	nr. N, S, M, F	N, S, M, F	—
lamellae 4th toe	nr. S, nr. M, F	nr. M	nr. M	S, nr. M, F
scansors 4th toe	S, nr. M, F	nr. M	to M	nr. S, M, F
lamellae 4th finger	S, nr. F	M, nr. F	M, nr. F	—
scansors 4th finger	S, F	nr. S, M, F	nr. S, M, F	—
preanal pores	M, F	M, F	M, F	—
D. pattern	S	S	F	?

TABLE 10 (*Contd.*)

Specimen	F, S 44 MC	F, S 31 SC	Mahé 45 MC	Seychelles 43 MC
E. Characters are in/near/to variation of				
North (only N)	4x	10x	5x	2x
Silhouette (only S)	15x (2x)	15x (1x)	8x	9x
Mahé (only M)	14x	20x (3x)	16x (3x)	8x
Frigate (only F)	20x (3x)	19x	19x (4x)	9x
F. Subspecific classification (according to weighted character affinities and subjective impression)	*longinsulae* or *umbrae* (Frigate or Silhouette)	*pulchra* or *longinsulae* (Mahé or Frigate)	*purchra* or *longinsulae* (Mahé or Frigate)	ssp.

A character of a specimen may fall into the variation of a population (as known from the specimens with definite locality data). If the character does not lie within this variation, it may nevertheless approximate it, which is defined as being near that variation ("nr."). Such proximity is assumed, if in relation to the known variation
— a head proportion is 0.05 close,
— a scale proportion is 0.5 close,
— the labial count is 1 scale more or less,
— another scale count is 2 scales more or less
If there is no proximity to any known variation, it is assumed that there is a tendency towards the population whose variation comes closest (= "to").
N = North
S = Silhouette
M = Menai
F = Frigate

TABLE 11

VARIATION OF ALL SPECIMENS

taxon specimens BSRC Geck	*longinsulae* (5) 36, 40, 41, 49, 51 SC	Seychelles (18) 31 SC, 43, 44, 45 MC	*menaiensis* (2) 68, 69 SC	all subspecies (20) all specimens
SVL	41 –57	41 –57	58 –61	
SVL/TL	1.15	1.15– 1.31	—	
LH/RE	1.79– 1.87	1.77– 1.94	1.81	
LH/NE	2.05– 2.36	2.05– 2.44	2.08– 2.27	
LH/WH	1.58– 1.62	1.43– 1.72	1.4 – 1.61	
LH/HH	2.18– 2.6	2.18– 2.6	1.86– 2.42	
WH/HH	1.36– 1.62	1.34– 1.64	1.325–1.5	
NE/HH	1.02– 1.1	0.97– 1.1	0.89– 1.33	
L/D	1 – 2.33	1 –2.5	1.33– 2	
H.1000/SVL	6.00– 8.77	5.45–11.11	3.44– 5.56	
N.1000/SVL	1.85– 3.51	1.72– 3.64	1.72– 2.46	
D.1000/SVL	2.88– 3.70	1.92– 5.45	4.92– 5.17	
L.1000/SVL	3.66– 7.41	3.63– 9.62	6.89– 9.84	
V.1000/SVL	9.26–14.81	7.27–14.81	11.48–13.79	
G.1000/SVL	1.85– 2.78	1.79– 3.64	2.58– 3.28	
scales around midbody	78 –92	70 –98	88 –90	
supralabials	8 –11	8 –12	8 – 9	
sublabials	7 – 9	7 – 9	7 – 8	
lamellae 4th toe	20 –26	20 –30	21 –22	
scansors 4th toe	10 –15	10 –18	12 –13	
lamellae 4th finger	18 –22	17 –23	18 –19	
scansors 4th finger	9 –13	9 –14	11	
preanal pores	10 –15/	6 –16/	11 –15/	

taxon specimens BSRC Geck	*rubra* (2) 29, 50 SC	*umbrae* (3) 32, 42, 30 SC	*pulchra* (4) 35, 38, 48, 70 SC
SVL	43 –55	43 –55	49 –59
SVL/TL	1.16	1.31	—
LH/RE	1.88– 1.94	1.84– 1.91	1.77– 1.89
LH/NE	2.40– 2.44	2.18– 2.43	2.19– 2.35
LH/WH	1.67– 1.71	1.62– 1.72	1.49– 1.58
LH/HH	2.44– 2.46	2.39– 2.48	2.19– 2.52
WH/HH	1.43– 1.45	1.39– 1.5	1.43– 1.6
NE/HH	1 – 1.02	1.02– 1.1	0.97– 1.08
L/D	1 – 2	1.33– 1.5	2 – 2.5
H.1000/SVL	6.98– 7.27	7.27–11.11	8.16–10.01
N.1000/SVL	1.82– 2.33	2.0 – 3.64	1.72– 3.64
D.1000/SVL	3.64– 4.65	4.0 – 5.45	2.58– 4.08
L.1000/SVL	4.65– 7.27	4.65– 7.27	5.17– 9.67
V.1000/SVL	9.09– 9.30	10.91–13.33	10.34–13.79
G.1000/SVL	2.33– 3.64	1.82– 2.33	2.73– 3.45

TABLE 11 (*Contd.*)

scales around midbody	70	–76		76	–98	76	–88
supralabials	8	– 9		7	– 9	9	–12
sublabials	7	– 8		7	– 8	7	– 9
lamellae 4th toe	24			21	–24	22	–28
scansors 4th toe	12			11	–13	12	–14
lamellae 4th finger	18			17	–18	21	–23
scansors 4th finger	10			9	–10	12	–14
preanal pores	—			6	– 9/	8	–16/

stouter form of Assumption (named by Cheke: *Phelsuma abbotti sumptio,* now considered to be a valid species, see below).

The dorsal and lateral scales of body and tail are wide spaced, which is a unique character of this species. The back is dull green to dull blue (olive-green to blue-green in life), sometimes with a dull red-brown broad vertebral line or such spots mainly in the vertebral region. Flanks and legs are brownish with lighter yellowish-brown, rounded spots in a dark grey network. The head has a preocular red semicircle, which continues interocularly; this figure is never V-shaped, but always rounded. On the back of the head there are some irregular, usually transversally enlarged dark redbrown spots. A dark redbrown streak runs from the nostril to the eye and continues behind the eye towards the occiput in a U-shaped figure. A second stripe starts on the second row of postmentals, continues from the inframaxillariae to the posterior labials and to the ear and then forms a second, though interrupted U-figure on the anterior nape. Between these two dark stripes the temple is whitish. A third similar figure is formed by the inner dark stripe of the anterior throat, but this stripe continues to the side of the neck only and is usually not visible there in life. Usually there is a third dark semicircle on the inner throat. All these gular stripes are ventrally dark grey and laterally and dorsally dark redbrown or greybrown. Underneath the animal is white, but may be slightly yellowish in the anal and femoral region.

The meristic data of the holotype, whose pattern has faded in alcohol, are given in table 12.

An earlier description is given by Krefft (1907), cf. also Boettger (1881, part.); Mertens (1964, 1966 part.). Published photos referred to this species are found in Mertens (1962, fig.) and Nietzke (1972, fig. 73). All previous authors have included this species under the name *Phelsuma abbotti.*

5. **Phelsuma befotakensis** sp nov.
BSRC Geck 82 SC (Holotype),
80-81 SC (Paratypes)

Type locality and d.n.: Befotaka, Northwest Madagascar (s. of Presqu' Ile Radama, *c.* halfway between Diégo Suarez and Majunga; not the village on Nosy Bé!).

Diagnosis: The meristic data are given in table 20.

The adhesive pads of the species are not as wide as those of *Phelsuma chekei.*

Ground colour is a bluish green, which in the light phase may turn to a yellowish bright green mid-dorsally and on the sacrum.

A dark redbrown stripe runs from the nostril through the eye and continues upwards through the temple in order to form the dorsolateral redbrown stripe on the nape; it continues as a series of elongated spots which

TABLE 12

Phelsuma chekei, DIEGO SUAREZ

specimen BSRC Geck	20 MC	33 MC	36 MC	variation
sex	♂	♀	♂	—
SVL	58	55	60	55 –60
TL	"65"	52	74	52 –74
SVL/TL	—	0.945	1.23	0.94– 1.23
LH	15.2	13.7	15.4	13.7 –15.4
RE	7.9	7.2	8.6	7.2 – 8.6
NE	7.2	6.2	6.9	6.2 – 7.2
WH	10.5	10.0	11.0	10.0 –11.0
HH	7.2	6.9	6.7	6.7 – 7.2
LH/RE	1.92	1.90	1.79	1.79– 1.92
LH/NE	2.17	2.21	2.23	2.17– 2.23
LH/WH	1.45	1.37	1.64	1.37– 1.64
LH/HH	2.17	1.99	2.30	1.99– 2.30
WH/HH	1.46	1.45	1.64	1.45– 1.64
NE/HH	1	0.90	1.03	0.90– 1.03
gran.: H	0.4	0.5	0.4	0.4 – 0.5
N	0.2	0.2	0.2	0.2
D	0.3	0.3	0.3	0.3
L	0.7	0.5	0.5	0.5 – 0.7
V	0.8	0.8	0.8	0.8
G	0.15	0.15	0.1	0.1 – 0.15
L/D	2.33	1.67	1.67	1.67– 2.33
H.1000/SVL	6.90	9.09	6.67	6.67– 9.09
N.1000/SVL	3.45	2.73	3.33	2.73– 3.45
D.1000/SVL	5.17	5.45	5	5 – 5.45
L.1000/SVL	12.06	9.09	8.33	8.33–12.06
V.1000/SVL	13.79	14.54	13.33	13.33–14.54
G.1000/SVL	2.59	2.73	1.67	1.67– 2.73
scales around midbody	70	68	72	68 –72
supralabials r/l	7/6	8/7	8/9	6 – 9
sublabials r/l	7	8	7/9	7 – 9
lamellae 4th toe	21	21	23	21 –23
scansors 4th toe	10	11	12	10 –12
lamellae 4th finger	19	19	19	19
scansors 4th finger	10	11	11	10 –11
preanal pores r/l	17/17	—	12/14 p	12 –17

separate dorsum and flanks and which may fade in the light phase. A red vertebral stripe starts on the occiput and continues to the base of the tail. A second smaller redbrown stripe, which joins the dorsolateral stripe on the anterior nape, originates in the outer dark chin stripe and runs through the ear. The inner gular stripe is not evident on the sides of the neck. Neck and body show greenish, in the light phase even yellowish rounded spots in

longitudinal rows: one between the vertebral and the dorsolateral redbrown stripes, another below the dorsolateral stripe on the upper flank and a third indistinct one on the lower flank. In the dark phase the light spots on the upper flank are encircled by irregular dark red spots, which gives the impression of ocelli. The same sort of spots are present on the legs. A conspicuous character is a redbrown prefrontal stripe from the scales behind the intranasal granule all along the fore head; before the eyes it merges with a U-shaped inter-

TABLE 13

Phelsuma befotakensis, BEFOTAKA

specimen BSRC Geck	80 SC	81 SC	82 SC	variation
sex	♂	♀	♂	—
SVL	48	44	48	44 –48
TL	*c.* 70	*c.*60	—	60 –70
SVL/TL	1.46	1.36	—	1.36– 1.46
LH	13.3	13.6	13.0	13.0 –13.6
RE	7.2	7.5	7.0	7.0 – 7.5
NE	6.1	6.4	6.0	6.0 – 6.4
WH	8.1	8.9	9.8	8.1 – 9.8
HH	6.0	5.8	6.3	5.8 – 6.3
LH/RE	1.85	1.81	1.86	1.81– 1.86
LH/NE	2.18	2.12	2.17	2.12– 2.18
LH/WH	1.35	1.52	1.33	1.33– 1.52
LH/HH	2.22	2.34	2.06	2.06– 2.34
WH/HH	1.35	1.53	1.33	1.33– 1.53
NE/HH	1.02	1.10	0.95	0.95– 1.10
gran.: H	0.4	0.5	0.5	0.4 – 0.5
N	0.15	0.2	0.3	0.15– 0.3
D	0.3	0.4	0.4	0.3 – 0.4
L	0.5	0.5	0.5	0.5
V	0.5	0.8	0.75	0.5 – 0.8
G	0.15	0.25	0.15	0.15– 0.25
L/D	1.67	1.25	1.25	1.25– 1.67
H.1000/SVL	8.33	11.36	10.42	8.33–11.36
N.1000/SVL	3.125	4.54	5.25	3.125–5.25
D.1000/SVL	6.25	9.09	8.33	6.25– 9.09
L.1000/SVL	10.42	11.36	10.42	10.42–11.36
V.1000/SVL	10.42	18.18	15.625	10.42–18.18
G.1000/SVL	3.125	3.41	3.125	3.125–3.41
scales around midbody	78	74	74	74 –78
supralabials r/l	8/7	6/7	9	6 – 9
sublabials r/l	7	7/8	7/6	6 – 8
lamellae 4th toe	20	22	22	20 –22
scansors 4th toe	10	11	13	10 –13
lamellae 4th finger	22	20	18	18 –22
scansors 4th finger	12	10	10	10 –12
preanal pores r/l	15/17	—	10	10 –17/

TABLE 14

VARIATION OF *Phelsuma sundbergi*

specimens BSRC Geck	Praslin (1) 8 SC	Félicité (4) 28, 33, 45, 47 SC	La Digue (8) 43, 44, 46, 71-74, 27 SC	Total (13)
SVL	74	54 –67	62 –77	54 –77
SVL/TL	1.19	—	1.27– 1.28	1.19– 1.28
LH/RE	1.84	1.84– 1.96	1.71– 1.93	1.71– 1.96
LH/NE	2.22	2.2 – 2.33	1.95– 2.37	1.95– 2.37
LH/WH	1.47	1.41– 1.6	1.31– 1.61	1.31– 1.61
LH/HH	2.14	2.05– 2.4	2.08– 2.43	2.05– 2.43
WH/HH	1.46	1.41– 1.51	1.37– 1.65	1.37– 1.65
NE/HH	0.96	0.91– 1.09	0.95– 1.39	0.91– 1.39
L/D	1.67	1.67– 2.5	1.13– 2.5	1.13– 2.5
H.1000/SVL	13.51	7.4 –10.77	7.58–12.31	7.4 –13.51
N.1000/SVL	4.05	1.8 – 4.24	2.46– 4	1.8 – 4.24
D.1000/SVL	4.05	3.28– 4.48	3.03– 5.38	3.03– 5.38
L.1000/SVL	6.76	7.4 – 9.23	5.3 – 8.2	5.3 – 9.23
V.1000/SVL	13.51	8.26–12.31	9.84–15.38	8.26–15.38
G.1000/SVL	4.05	3.28– 4.48	2.64– 4.8	2.64– 4.8
scales around midbody	88	76 –88	88 –100	76 –100
supralabials	10/11	8 –11	8 –10	8 –11
sublabials	8	7 – 9	7 – 9	7 – 9
lamellae 4th toe	22	23 –29	21 –31	21 –31
scansors 4th toe	11	13 –16	10 –18	10 –18
lamellae 4th finger	—	19 –26	19 –25	19 –26
scansors 4th finger	13	11 –16	10 –17	10 –17
preanal pores	13–14	13 –15	10 –16	10 –16

ocular series of spots. A second series of spots forms an opposite U with the tip on the occiput and the ends on the supraocular scales. Underneath the animal is yellowish white, with a yellowish anal and femoral region.

The meristic data of the holotype, which shows the characteristic pattern, are given in table 13.

The female paratype (Geck 81 SC) contains two well developed eggs.

Earlier references to this species may be included under the name *Phelsuma abbotti.*

6. **Phelsuma sundbergi**

This green *Neophelsuma* species is found on the Praslin Bank of the Seychelles and on Marie Louise of the Amirante Islands (cf. Cheke 1982, in press). It is distinguished from other species by the following characters: Large size (-8 cm SVL), wider snout angle (cf. Cheke 1982) keeled chest scales, and unique pattern: Besides a dark streak from the nostril to the eye there usually is a shaped pre- and interocular figure on the head; the distinct dark red mottling on the posterior dorsum and sacrum consists of small longitudinal spots (-2.0 mm wide), which may have fused transversally and longitudinally to form a red network; chin and throat may turn yellowish and show an outer dark, eventually broken semicircle and a few irregular spots in this figure;

TABLE 15

Phelsuma sundbergi, FELICITE

specimen BSRC Geck	28 SC	33 SC	45 SC	47 SC	variation
sex	♀	♂	♀	♀	
SVL	54	65	67	61	54 –67
TL	"57"	"81"	"84"	"58"	—
SVL/TL	—	—	—	—	—
LH	13.4	15.5	16.4	14.7	13.4 –16.4
RE	7.0	8.4	8.8	7.5	7.0 – 8.8
NE	6.0	7.0	7.3	6.3	6.0 – 7.3
WH	8.5	10.6	11.6	9.5	8.5 –11.6
HH	5.5	7.0	8.0	6.3	5.5 – 8.0
LH/RE	1.9	1.84	1.86	1.96	1.84– 1.96
LH/NE	2.2	2.21	2.25	2.33	2.2 – 2.33
LH/WH	1.6	1.46	1.41	1.55	1.41– 1.6
LH/HH	2.4	2.21	2.05	2.33	2.05– 2.4
WH/HH	1.5	1.51	1.41	1.51	1.41– 1.51
NE/HH	1.09	1	0.91	1	0.91– 1.09
gran.: H	0.4	0.7	0.6	0.6	0.4 – 0.7
N	0.1	0.2	0.2	0.25	0.1 – 0.25
D	0.2	0.3	0.3	0.2	0.2 – 0.3
L	0.4	0.6	0.5	0.5	0.4 – 0.6
V	0.5	0.8	0.8	0.6	0.5 – 0.8
G	0.2	0.3	0.3	0.2	0.2 – 0.3
L/D	2	2	1.67	2.5	1.67– 2.5
H.1000/SVL	7.4	10.77	9.00	9.84	7.4 –10.77
N.1000/SVL	1.8	3.08	2.99	4.24	1.8 – 4.24
D.1000/SVL	3.7	3.69	4.48	3.28	3.28– 4.48
L.1000/SVL	7.4	9.23	7.46	8.20	7.4 – 9.23
V.1000/SVL	8.26	12.31	11.94	9.84	8.26–12.31
G.1000/SVL	3.7	3.69	4.48	3.28	3.28– 4.48
scales around midbody	86	88	82	76	76 –88
supralabials r/l	10/11	10/9	10/8	8/9	8 –11
sublabials r/l	9/8	8/7	9/7	7/8	7 – 9
lamellae 4th toe	23	29	25	26	23 –29
scansors 4th toe	13	16	15	13	13 –16
lamellae 4th finger	23	26	25	19	19 –26
scansors 4th finger	13	16	14	11	11 –16
preanal pores r/l	—	15/15	*c.* 15/15 p	*c.* 13/13 p	13 –15

femoral and anal region may turn yellowish or orange (especially in males), while the usual ventral colour is an indistinct white; legs are mottled with a slightly darker greyish or brownish green.

Our specimens, also living ones, were collected on Praslin, La Digue and Félicité and show the following geographic variation (for biometric data see tables 14-17):

The specimens from Praslin are usually

TABLE 16A

Phelsuma sundbergi, LA DIGUE

specimen BSRC Geck	43 SC	44 SC	46 SC	71 SC	72 SC
sex	♀	♂	♂	♀	♂
SVL	62	66	77	68	65
TL	79	"82"	"72"	"80"	"44"
SVL/TL	1.27	—	—	—	—
LH	15.0	16.6	17.0	16.8	17.0
RE	8.2	9.0	8.8	10.0	9.7
NE	7.6	7.0	7.8	8.1	8.7
WH	9.3	10.5	12.1	11.7	11.0
HH	6.8	7.4	7.9	8.1	7.0
LH/RE	1.83	1.84	1.93	1.68	1.75
LH/NE	1.97	2.37	2.18	2.07	1.95
LH/WH	1.61	1.58	1.40	1.44	1.55
LH/HH	2.21	2.24	2.15	2.1	2.43
WH/HH	1.37	1.42	1.53	1.46	1.57
NE/HH	1.12	0.95	0.99	1.01	1.24
gran.: H	0.6	0.5	0.6	0.7	0.8
N	0.2	0.2	0.3	0.2	0.25
D	0.3	0.2	0.4	0.3	0.35
L	0.4	0.4	0.45	0.5	0.5
V	0.7	0.8	0.9	0.7	1.0
G	0.25	0.3	0.3	0.2	0.3
L/D	1.33	2	1.13	1.67	1.43
H.1000/SVL	9.68	7.58	7.79	10.29	12.31
N.1000/SVL	3.23	3.03	3.90	2.94	3.85
D.1000/SVL	4.84	3.03	5.19	4.41	5.38
L.1000/SVL	6.45	6.06	5.84	7.35	7.69
V.1000/SVL	11.29	12.12	11.69	10.29	15.38
G.1000/SVL	4.03	4.54	3.90	2.94	4.62
scales around midbody	96	90	88	92	90
supralabials r/l	10/11	10	9	9/10	10
sublabials r/l	8/9	8/7	8/7	7/8	7
lamellae 4th toe	21	27	23	31	27
scansors 4th toe	10	14	12	18	14
lamellae 4th finger	21	23	19	25	25
scansors 4th finger	11	12	11	17	15
preanal pores r/l	—	13/14	10/11	—	16/

larger than those from the other islands. They show a lighter green dorsally, a lighter ventral coloration (white or slight yellowish) and a reduced pattern on the throat with fewer and less distinct markings.

On the contrary the specimens from La Digue and Félicité are usually smaller, and show a darker green dorsally, a darker ventral coloration (dark yellow or orange) and a broad dark pattern on the throat. The speci-

TABLE 16 B

Phelsuma sundbergi

specimen BSRC Geck	La Digue 73 SC	La Digue 74 SC	La Digue variation	La Digue or Félicité 27 SC
sex	♂	♀	—	♀
SVL	61	75	62 –77	63
TL	78	"78"	78 –79	"71"
SVL/TL	1.28	—	1.27– 1.28	—
LH	16.6	19.9	15.0 –19.9	15.2
RE	9.7	11.5	8.2 –11.5	8.4
NE	7.7	9.5	7.0 – 9.5	7.1
WH	11.4	15.2	9.3 –15.2	9.8
HH	7.0	9.3	6.8 – 9.3	7.3
LH/RE	1.71	1.73	1.71– 1.93	1.81
LH/NE	2.16	2.09	1.95– 2.37	2.14
LH/WH	1.46	1.31	1.31– 1.61	1.55
LH/HH	2.37	2.14	2.1 – 2.43	2.08
WH/HH	1.63	1.63	1.37– 1.65	1.34
NE/HH	1.39	1.02	0.95– 1.39	0.97
gran.: H	0.5	0.9	0.5 – 0.9	0.6
N	0.15	0.3	0.15– 0.3	0.2
D	0.3	0.4	0.2 – 0.4	0.2
L	0.5	0.6	0.4 – 0.6	0.4
V	0.6	1.0	0.6 – 1.0	0.8
G	0.15	0.3	0.15– 0.3	0.3
L/D	1.67	1.5	1.13– 2.0	2
H.1000/SVL	8.20	12	7.58–12.31	9.5
N.1000/SVL	2.46	4	2.46– 4	3.2
D.1000/SVL	4.92	5.3	3.03– 5.38	3.2
L.1000/SVL	8.20	8	5.84– 8.2	5.3
V.1000/SVL	9.84	13.3	9.84–15.38	12.7
G.1000/SVL	2.64	4	2.64– 4.62	4.8
scales around midbody	100	98	88 –100	90
supralabials r/l	9	8/9	8 –10	9
sublabials r/l	7	7	7 – 9	9/8
lamellae 4th toe	31	29	21 –31	26
scansors 4th toe	16	16	10 –18	13
lamellae 4th finger	25	19	19 –25	23
scansors 4th finger	15	10	10 –17	13
preanal pores r/l	p	—	10 –16/	—

mens from La Digue and Félicité do not differ from each other in coloration, but perhaps the specimens from Félicité are smaller on the average than those from La Digue. The two populations may be fairly easily separated by the number of scales around midbody, which is less than 88 for Félicité and more than 88 for La Digue. By the number of scales around

TABLES 17, 18

	P. sundbergi, PRASLIN	*P. mad. kochi*, MAJUNGA
specimen BSRC Geck	8 SC	7 SC
sex	♂	♂
SVL	74	65
TL	80	69
SVL/TL	1.19	1.06
LH	18.2	16.8
RE	9.9	9.5
NE	8.2	8.0
WH	12.4	10.8
HH	8.5	7.4
LH/RE	1.84	1.77
LH/NE	2.22	2.1
LH/WH	1.47	1.56
LH/HH	2.14	2.27
WH/HH	1.46	1.46
NE/HH	0.96	1.19
gran.: H	1.0	0.6
N	0.3	0.2
D	0.3	0.4
L	0.5	0.4
V	1.0	0.7
G	0.3	0.1
L/D	1.67	1
H.1000/SVL	13.51	9.23
N.1000/SVL	4.05	6.15
D.1000/SVL	4.05	6.15
L.1000/SVL	6.76	7.69
V.1000/SVL	13.51	10.77
G.1000/SVL	4.05	1.54
scales around midbody	88	86
supralabials r/l	10/11	10
sublabials r/l	8	8/9
lamellae 4th toe	22	25
scansors 4th toe	11	14
lamellae 4th finger	—	20
scansors 4th finger	13	12
preanal pores r/l	—	14/13

midbody, the Praslin animals can be separated neither from the La Digue nor from the Félicité animals.

At present we do not think it appropriate to distinguish subspecies in *Phelsuma sundbergi*, and therefore we place the name *Phelsuma madagascariensis (sundbergi) ladiguensis* Böhme & Meier 1982 into the synonymy of *Phelsuma sundbergi* (the availability of the name is doubtful in respect of Artt. 5, 6, 10 lit. b, 11 lit. c International Rules for Zoological Nomenclature; this question is definitely left open).

7. **Phelsuma madagascariensis**

This species shows considerable variation in its range, as is demonstrated by our specimens (cf. tables 18, 19). They seem to stem from different localities.

BSRC Geck 7 SC is from Majunga and must be referred to *Phelsuma madagascariensis kochi* on the basis of its coloration, pattern and biometric data; the same is true for a living specimen.

BSRC Geck 8, 13 MC are both *Phelsuma madagascariensis grandis*. The specimens belong to the series of several generations bred by the senior author and agree with the variation known for that subspecies.

The other alcohol specimens should not be assessed to a subspecies, as we definitely think that the amount of subspecific and intrasubspecific variation is not yet reliably described. These non-assignable specimens are included to give an idea of the specific variation in *Phelsuma madagascariensis* (ex. *kochi*).

BIOGEOGRAPHY AND PHYLOGENY

Madagascar is the center of evolution of the genus *Phelsuma*. It has already been shown, that the subgenus *Phelsuma* (*Archaeophelsuma*) on the Mascarene Islands consists of old relict forms surviving on the ancient periphery of the generic distribution and that the forms of *Neophelsuma* found outside Madagascar are more recent invaders (Börner 1972). As it may be presumed that the rate of evolu-

TABLE 19

Phelsuma madagascariensis SSPP. (EXCL. *kochi*)

specimen BSRC Geck	8 MC	13 MC	53 MC	55 MC	56 MC	variation
sex	semiad., ♂?	iuv.	♀	♀	♂	—
SVL	79	31	102	83	83	31 –102
TL	"82"	30	113	"42"	101	30 –113
SVL/TL	—	0.97	1.11	—	1.22	0.97– 1.22
LH	21.4	9.6	23.2	21.8	25.5	9.6 –25.5
RE	13.3	5.3	13.6	12.6	14.7	5.3 –14.7
NE	10.7	4.4	11.5	10.6	12.0	4.4 –12.0
WH	14.5	7.2	16.0	17.0	17.8	7.2 –17.8
HH	10.3	4.3	9.6	12.0	12.3	4.3 –12.3
LH/RE	1.61	1.81	1.71	1.73	1.73	1.61– 1.81
LH/NE	2.0	2.18	2.02	2.05	2.13	2.0 – 2.18
LH/WH	1.48	1.33	1.45	1.28	1.43	1.28– 1.48
LH/HH	2.08	2.23	2.41	1.82	2.01	1.82– 2.41
WH/HH	1.41	1.67	1.67	1.42	1.45	1.41– 1.67
NE/HH	1.04	1.02	1.20	0.88	0.98	0.88– 1.20
gran.: H	0.7	—	0.7	0.5	0.8	0.5 – 0.8
N	0.3	—	0.5	0.4	0.5	0.3 – 0.5
D	0.6	—	0.6	0.4	0.5	0.4 – 0.6
L	1.0	—	1.7	1.3	1.0	1.0 – 1.7
V	1.5	—	1.4	0.8	1.0	0.8 – 1.5
G	0.4	—	0.6	0.4	0.5	0.4 – 0.6
L/D	1.67	—	3.40	4.33	2	1.67– 4.33
H.1000/SVL	8.86	—	6.86	5.02	9.64	5.02– 9.64
N.1000/SVL	3.80	—	4.90	4.82	6.02	3.80– 6.02
D.1000/SVL	7.59	—	4.90	3.61	6.02	3.61– 7.59
L.1000/SVL	12.66	—	16.67	15.66	12.05	12.05–16.67
V.1000/SVL	20.25	—	13.73	9.64	12.05	9.64–20.25
G.1000/SVL	5.06	—	5.88	4.82	6.02	4.82– 6.02
scales around midbody	82	—	92	86	84	82 –92
supralabials r/l	10	9/8	7/8	9	9/8	7 –10
sublabials r/l	8/7	7	8/7	7/8	8	7 – 8
lamellae 4th toe	28	—	21	18	20	18 –28
scansors 4th toe	16	15	17	13	14	13 –17
lamellae 4th finger	22	24	21	16	23	16 –24
scansors 4th finger	13	12	15	11	15	11 –15
preanal pores r/l	—	—	15/17 p	16/16 p	21/21	15 –21/

tion in the subgenus *Neophelsuma* and its species groups is nearly equal throughout the subgenus, it is possible to conclude that the extent of character deviation in a given taxon proves the duration of its separate evolution. On this scale the *Phelsuma astriata* ancestor, a form related to *Phelsuma lineata,* was the earliest arrival in the Seychelles; *Phelsuma astriata* is considered to form a species group of its own (Börner 1972). The *Phelsuma longinsulae*

TABLE 20

SYNOPTIC TABLE OF THE VARIATION OF ADULT SPECIMENS IN THE *Phelsuma madagascariensis* SPECIES GROUP

taxon	*madagascariensis kochi* (1)	*madagascariensis* ssp. (4) (excl. *kochi*)	*sundbergi* (13)
SVL	65	79 –10.2	54 –77
SVL/TL	1.06	1.11– 1.22	1.19– 1.28
LH/RE	1.77	1.61– 1.73	1.71– 1.96
LH/NE	2.1	2.0 – 2.13	1.95– 2.37
LH/WH	1.56	1.28– 1.48	1.31– 1.61
LH/HH	2.27	1.82– 2.41	2.05– 2.43
WH/HH	1.41	1.41– 1.67	1.37– 1.65
NE/HH	1.19	0.88– 1.20	0.91– 1.39
L/D	1	1.67– 4.33	1.13– 2.5
H.1000/SVL	9.23	5.02– 9.64	7.4 –13.51
N.1000/SVL	6.15	3.80– 6.02	1.8 – 4.24
D.1000/SVL	6.15	3.61– 7.59	3.03– 5.38
L.1000/SVL	7.69	12.05–16.67	5.3 – 9.23
V.1000/SVL	10.77	9.64–20.25	8.26–15.38
G.1000/SVL	1.54	4.82– 6.02	2.64– 4.8
scales around midbody	86	82 –92	76 –100
supralabials	10	8 –10	8 –11
sublabials	8/9	7 – 8	7 – 9
lamellae 4th toe	25	18 –28	21 –31
scansors 4th toe	14	13 –17	10 –18
lamellae 4th finger	20	16 –23	19 –26
scansors 4th finger	12	11 –15	10 –17
preanal pores	—	15 –21/	10 –16/

ancestors arrived next, the *Phelsuma sundbergi* ancestor last.

Phelsuma sundbergi is closest to *Phelsuma madagascariensis kochi;* the Praslin population, from which the La Digue and Félicité populations are derived, is hardly distinguishable from Malagasian *Phelsuma madagascariensis kochi.* The main differences are only the condition of the chest scales (usually keeled scales in *Phelsuma sundbergi,* unkeeled scales in *Phelsuma madagascariensis kochi*), the length of the tail (long v. short), the flank colour (green v. brownish green with eventual white spots), and the dorsal pattern (smaller elements in vermiculation v. red spots).

The other Malagasian forms of *Phelsuma madagascariensis* (ex. *kochi*) have intermediary lengths of tails and green flanks like *Phelsuma sundbergi.* These resemblances seem to be due to a convergent evolution, as there are so many differences between *Phelsuma sundbergi* and *Phelsuma madagascariensis* (ex. *kochi*): *Phelsuma sundbergi* is smaller, especially its La Digue and Félicité specimens; its head and scale proportions, especially the L/D ratio, are usually closer to *Phelsuma madagascariensis kochi* than to *Phelsuma madagascariensis* ssp.; *Phelsuma sundbergi* has a yellow orange belly colour, a dark chin pattern and dark red dorsal pattern elements, being closer to *Phelsuma*

TABLE 20 (*Contd.*)

taxon	*andamanensis* (3)	*longinsulae* spp (18) Seychelles	*l. menaiensis* (2)	*chekei* (3)	*befotakensis* (3)
SVL	42 –56	41 –57	58 –61	55 –60	44 –48
SVL/TL	1.09– 1.40	1.15– 1.31	—	0.94– 1.23	1.36– 1.46
LH/RE	1.73– 1.89	1.77– 1.94	1.81	1.79– 1.92	1.81– 1.86
LH/NE	2.04– 2.15	2.05– 2.44	2.08– 2.27	2.17– 2.23	2.12– 2.18
LH/WH	1.47– 1.6	1.43– 1.72	1.4 – 1.61	1.37– 1.64	1.33– 1.53
LH/HH	2.14– 2.42	2.18– 2.6	1.86– 2.42	1.99– 2.30	2.06– 2.34
WH/HH	1.42– 1.64	1.34– 1.64	1.325–1.5	1.45– 1.46	1.33– 1.53
NE/HH	1.05– 1.10	0.97– 1.1	0.89– 1.33	0.9 – 1.03	0.95– 1.10
L/D	1 – 2.5	1 – 2.5	1.33– 2	1.67– 2.33	1.25– 1.67
H.1000/SVL	6.25– 7.14	5.45–11.11	3.44– 5.56	6.67– 9.09	8.33–11.36
N.1000/SVL	2.08– 2.69	1.72– 3.64	1.72– 2.46	2.73– 3.45	3.125–5.25
D.1000/SVL	3.57– 5.21	1.92– 5.45	4.92– 5.17	5 – 5.45	6.25– 9.09
L.1000/SVL	4.76– 8.93	3.63– 9.62	6.89– 9.84	8.33–12.06	10.42–11.36
V.1000/SVL	11.46–12.5	7.27–14.81	11.48–13.79	13.33–14.54	10.42–18.13
G.1000/SVL	2.08– 6.25	1.79– 3.64	2.58– 3.28	1.67– 2.73	3.125–3.41
scales around midbody	80 –90	70 –98	88 –90	68 –72	74 –78
supralabials	9 –11	8 –12	8 – 9	6 – 9	6 – 9
sublabials	8 –10	7 – 9	7 – 8	7 – 9	6 – 8
lamellae 4th toe	21 –24	20 –30	21 –22	21 –23	20 –22
scansors 4th toe	10 –15	10 –18	12 –13	10 –12	10 –13
lamellae 4th finger	18 –22	17 –23	18 –19	19	18 –22
scansors 4th finger	10 –14	9 –14	11	10 –11	10 –12
preanal pores	13 –16/	6 –16/	11 –15/	12 –17/	10 –17/

madagascariensis kochi than to *Phelsuma madagascariensis* ssp. in these elements, too. Finally, the pattern on the temple, which is a continuation of the chin and throat pattern, is almost as pronounced in *Phelsuma sundbergi* as in *Phelsuma madagascariensis kochi*, while it is much less distinct (faded or reddish instead of grey/black) or even lacking in the *Phelsuma madagascariensis* ssp.

Because of its smaller size, its dark spotted flanks, dark (even bluish) green dorsal colour and brick red pattern elements, its yellow anal region, its chin pattern, its short tail and short snout, and its scarcely enlarged laterals (L/D ratio), *Phelsuma madagascariensis kochi* should be considered as the most primitive member of the subgroup of large (6 cm SVL +) green forms, whose reduced dorsal patterns show transversal tendencies, the *Phelsuma madagascariensis* subgroup.

These above-mentioned characters of *Phelsuma madagascariensis kochi* are usually even more pronounced in the subgroup of small (-6 cm SVL) dark forms, whose extent dorsal patterns show longitudinal tendencies, the *Phelsuma abbotti* subgroup.

Therefore, *Phelsuma madagascariensis kochi* represents a phenotype derived from the taxon constituting the linkage between the two subgroups. *Phelsuma madagascariensis kochi* may

well represent a species of its own, but the final evaluation of its status must be the result of an extensive study of the total variation of *Phelsuma madagascariensis* in Madagascar.

Phelsuma madagascariensis (ex. *kochi*) and *Phelsuma sundbergi* reflect a parallel evolution from that ancestor in tail length, snout length, differentiation of laterals from dorsals and flank colour, and in the yellow factor (which brightens colour and pattern on the dorsum) though achieving different degrees of evolution in these characters. These two species reflect a divergent evolution from the ancestor in SVL (tendency towards a smaller size in *Phelsuma sundbergi* and towards a larger size in *Phelsuma madagascariensis*) and ventral colour and pattern (pronounced chin pattern and pronounced anal coloration in *Phelsuma madagascariensis*).

The phylogeny of the *Phelsuma abbotti* subgroup is even more complicated, but it is revealed by the character divergence of the forms, their geographic location and contemporary thinking on probabilities and chances of dispersal. In our opinion the clue to the phylogeny are the forms occurring on the Seychelles.

On the outer islands North and Silhouette and to a lesser extent on Frigate there are slender small geckos (*c.* 5 cm SVL) with a long head, a smooth transition from the small dorsals to the slightly enlarged laterals (L/D = *c.* 1-2) and few differentiated scales (labials, scansors, preanal pores). These characters are shared by the northwest Malagasian *Phelsuma befotakensis* as well as by *Phelsuma v-nigra* (including *Phelsuma robertmertensi*) from the Comoro Islands and also by *Phelsuma abbotti* from Aldabra. These forms primarily differ in their dorsal body pattern:

The forms from North and Silhouette Islands (*Phelsuma longinsulae rubra* resp. *umbrae*) and to a certain extent those from Frigate (*Phelsuma longinsulae longinsulae*) are bright green dorsally and have bright red dorsal marks. The forms from the Comoro Islands and *Phelsuma befotakensis* may assume a similar dorsal coloration, but usually show a bluish hue or are distinctly bluish. In this dark phase, the dorsal pattern is dark redbrown and the flanks may be dark grey-blue. The dorsal and lateral ocelli of *Phelsuma befotakensis* are greyish in the dark phase and yellowish in the light phase.

This survey of the dorsal colours demonstrates that the Malagasian *Phelsuma befotakensis* here retains the most primitive trait. Its ancestor gave rise to the Comoro forms, which are quite close : The yellow ocelli (which are arranged in longitudinal rows and which partly may fuse to form stripes, especially a vertebral stripe) formed the red pattern, while the tendency to a predominantly bluish ground colour persisted. The forms from the outer Seychelles are more advanced, as they intensified the yellow tendency of the ground colour. The yellow ocelli of *Phelsuma befotakensis* turned red, this state of evolution being demonstrated by the geckos from North Island, the most outlying island; a similar evolution took place in the Comoro Islands. In a second stage of evolution the red markings have been reduced, as they are very conspicuous in foliage dwelling forms (cf. Borner 1980). This tendency is demonstrated by the forms occurring on North Island, Silhouette and Frigate; even their ontogeny shows the reduction of red pattern: When a specimen of these forms grows older, the red pattern concentrates on the mid-dorsum and sacrum. The present day *Phelsuma befotakensis* also shows a modern trait, as its laterals (L/D ratio) are now enlarged a little more than those of the peripheral forms on the Comoro Islands and northern

Seychelles, a fact confirming the idea that the evolution is fastest in the center and slowest on the periphery of the range of the taxon.

Phelsuma abbotti from Aldabra Island is also considered to belong to this group. This latter species shows dark red dorsal markings on a dull greyish green or bluish grey dorsum and dark brown, nearly blackish flanks mottled with white spots; it has no ocelli on the flanks like *Phelsuma chekei.* This dark pattern serves to camouflage the trunk-base-dwelling gecko, of which Honegger reports that it lives sometimes in close association with the giant turtles, even taking refuge under their carapaces (cf. Blanc 1972, 591 referring to *Phelsuma barbouri* as a secondary ground dweller; the junior author has observed in Mauritius that *Phelsuma o. ornata* frequents the ground, too). So two explanations for this dark pattern are possible:

a) Either it represents a persisting trait of the ancestor to *Phelsuma befotakensis*; then the ancestor presumably had a darker coloration than *Phelsuma befotakensis,* which acquired its more bluish coloration and its capacity to show a "light", yellow phase after the colonization of Aldabra Island.

or

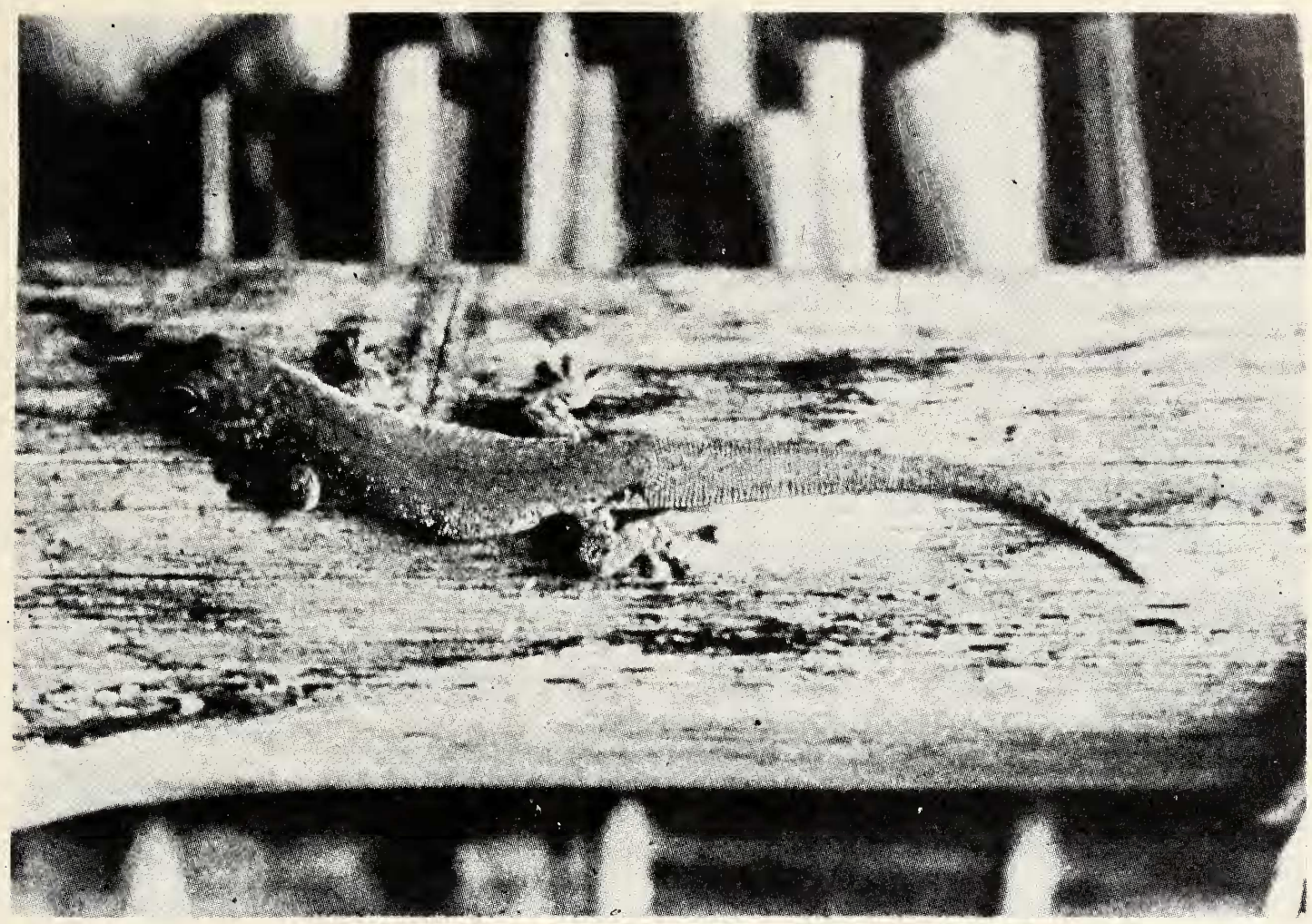
b) *Phelsuma abbotti* underwent a selection according to the specific conditions prevailing on Aldabra Island, and this selection has favoured a gecko "in its darkest phase".

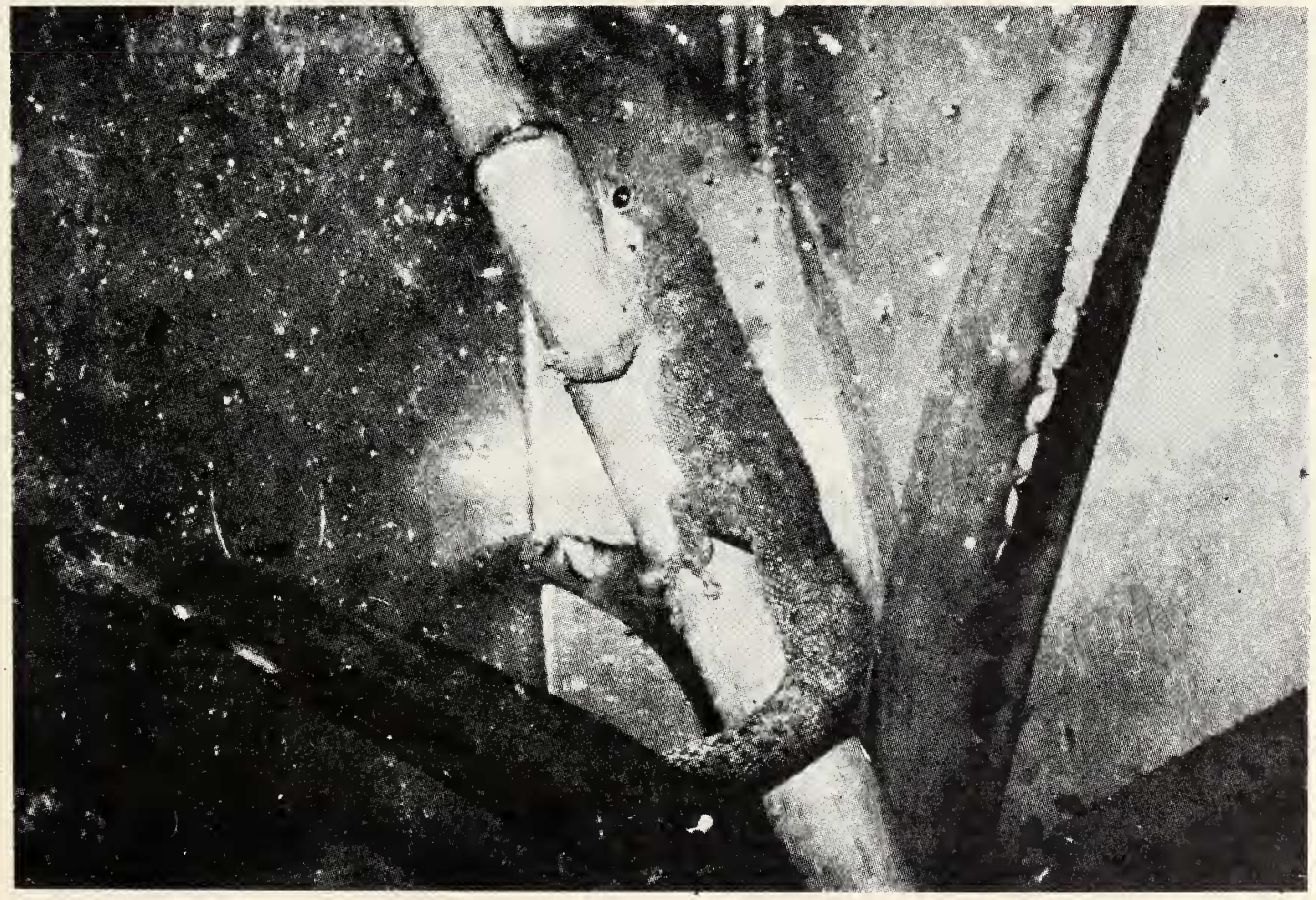
In our opinion none of these possible theories may be excluded, and both apply to explain the current situation: *Phelsuma abbotti* is an early off-shoot of the dark *Phelsuma befotakensis* ancestor, and subsequent selection favoured an even darker gecko. This theory is much more probable than the construction of an affinity with *Phelsuma chekei.* Both forms share only their dark colour, but they differ in proportions, scalation, and position of ocelli, which are characters of much greater consistency in island forms; *Phelsuma chekei* has ocelli on the flanks, but not *Phelsuma abbotti* (even true for juveniles), and *Phelsuma chekei* lacks any dorsal ocelli that may be related to the dark red ones of *Phelsuma abbotti;* juveniles of *Phelsuma abbotti* show a green dorsum earlier than those of *Phelsuma chekei.* Moreover, *Phelsuma abbotti* and *Phelsuma befotakensis* share the basic pattern (including the U-shaped stripe on the neck, the vertebral stripe, and the position of the ocelli, which are darker in *Phelsuma abbotti*).

The second assemblage in the *Phelsuma abbotti* subgroup is constituted by the large robust geckos (approx. 6 cm SVL) with a shorter head, a more abrupt transition from the small dorsals to the enlarged laterals (L/D: 1.5 - 2.5) and more differentiated scales (labials, scansors, preanal pores). These forms are found in North Madagascar (*Phelsuma chekei*), on Assumption Island (*Phelsuma sumptio*), on Menai Island, Cosmoledo Atoll (*Phelsuma longinsulae menaiensis*) and on Mahé, Seychelles (*Phelsuma longinsulae pulchra*).

They differ from each other mainly in dorsal coloration and pattern.

Phelsuma chekei has a greyish blue dorsum with dark red markings which may turn almost black in the dark phase, and a greyish pattern on the flanks. *Phelsuma sumptio* has a more bluish dorsum with faded dark red marks, the same vertebral stripe, and a reduced obscure mottling on the flanks; this may be described as "a concolorous type of *Phelsuma chekei*". But both forms differ in their ventral coloration (slightly yellowish in *Phelsuma chekei,* distinctly yellow or even orange in *Phelsuma sumptio*).





Above: P. abbotti; Aldabara Island. (*Photo*: P. Niedzwicki).
Below: P. sumptio; Assumption Island. (*Photo*: A.S. Cheke).

TABLE 21

LABIALS

		P. sundbergi	*P. madagascariensis*	*P. chekei*	*P. befotakensis*	*P. longinsulae*	*P. l. menaiensis*	*P. andamanensis*
Supralabials	6	0	0	1	1	0	0	0
	7	0	1	2	2	1	0	0
	8	3	3	2	1	6	2	2
	9	10	4	1	2	10	2	3
	10	10	4	0	0	6	0	1
	11	3	0	0	0	10	0	0
	12	0	0	0	0	0	0	0
	mean	9.5	8.9	7.5	7.7	9.5	8.5	8.8
Sublabials	6	0	1	0	1	1	0	0
	7	12	5	3	4	13	3	0
	8	10	5	2	1	15	1	2
	9	4	1	1	0	5	0	3
	10	0	0	0	0	0	0	1
	mean	6.7	7.5	7.7	7.0	7.7	7.3	8.8
difference between means		2.8	1.4	–0.2	0.7	1.8	1.2	0

Phelsuma longinsulae menaiensis and *Phelsuma longinsulae pulchra* are dull green dorsally and may show a bluish hue; their dorsal pattern is dull red. While *Phelsuma longinsulae menaiensis* usually shows some sort of dark and light flank mottling, this is usually lacking in *Phelsuma longinsulae pulchra.* Both forms also differ meristically.

Phelsuma longinsulae longinsulae is truly intermediate between the Mahé form *pulchra* and the northern forms *umbrae* and *rubra.* This situation is best explained by secondary intergradation: First the *Phelsuma befotakensis* — derivate arrived on the Seychelles and colonized all islands. Later in a second invasion the *Phelsuma chekei* — derivate arrived on Mahé where it interbred with the earlier arrivals. Some *Phelsuma chekei* — derivates or — more probably — some Mahé lizards of the combined type came to Frigate and influenced that gene-pool. The bright green colour and the intensive red markings stemming from the *Phelsuma befotakensis*-derivates turned duller under the influence of the bluish/black-red trend inherited from the *Phelsuma chekei*-derivates. The slender proportions of the early invaders turned more robust, and the primitive undifferentiated scalation of the early invaders turned to a more advanced state under the influence of the later arrivals. Therefore, the Mahé lizards now show characters intermediate between those of the forms from the northern islands and those of northern Malagasy, and the Frigate form is intermediary in the even smaller gap between the Mahé geckos and those from the northern islands. That a similar intergradation took place on tiny Menai Island is very improbable. We think it more probable that Menai was colonised by the new type from Mahé. This theory would be in

line with the close relation between the Mahé lizards and the Menai ones, with the fact that the Menai gecko shows an advanced scalation in comparison to the (parental) Mahé gecko and with the parallel case observed in *Phelsuma astriata*: *Phelsuma astriata* is found on the Seychelles and — in a derived form — on the tiny Astove Island (close to Menai Island), the latter form lacking a close relative on Madagascar.

This theory of two invasions of the Indian Ocean, meeting finally in the Seychelles, is in line with the evaluation of the two parental mainland forms *Phelsuma befotakensis* and *Phelsuma chekei* as species. In fact the basic structure of their patterns and their bluish dorsal ground colour (in *Phelsuma befotakensis* in the dark phase only) could be arguments for conspecificity, but on the other hand there are great differences in proportions, scalation and actual coloration and pattern, and these differences are more pronounced than those usually found in any two sibling species of a species group of this genus. Furthermore, our theory would explain the existence of the two pheno-types in the *Phelsuma abbotti*-subgroup.

This taxonomic assessment is in accordance with the species concept outlined by the junior author (Börner 1976/1982).

Another problem not yet discussed is the relation of *Phelsuma andamanensis*. Its position in the *Phelsuma madagascariensis* species group (Loveridge 1942, Mertens, Blanc 1972) has never been doubted. Its biometric data and the quality of its coloration and pattern clearly belong to the variation shown by the other forms of this species group, but *Phelsuma andamanensis* differs from all other members of the species group by the lack of enlarged postmentals.

Phelsuma andamanensis does not belong to the *Phelsuma madagascariensis* subgroup. Though its biometric data usually are in conformity with those of *Phelsuma sundbergi* and though especially the forms from La Digue and Félicité are similar in size and in ventral coloration, *Phelsuma andamanensis* lacks the wide head angle and the keeled chest scales of that species. The keeled chest scales are considered an advanced character and should therefore be present in a derived form, as should be the distinctive head angle. *Phelsuma madagascariensis* differs by size, shape and scalation (advanced state of laterals and preanal pores in *Phelsuma madagascariensis*). Both, *Phelsuma sundbergi* and *Phelsuma madagascariensis* (incl. *kochi*) tend to reduce the red pattern to the sacral region, and both (ex. *kochi*) show red patterns with a distinct tendency towards a transversal arrangement. In contrast to these tendencies *Phelsuma andamanensis* has a red neck pattern and an irregularly longitudinally arranged pattern on the posterior dorsum.

Phelsuma andamanensis is closer to the *Phelsuma abbotti* subgroup, in which the longitudinally arranged dorsal pattern prevails. Within this subgroup, *Phelsuma andamanensis* is nearest to the forms occurring on the islands Silhouette, North and Frigate. *Phelsuma andamanensis* seems to originate from the first Seychelles invader: The ancestor species of *Phelsuma befotakensis* increased its size, the number of scales (except preanal pores, see below), and the yellow factor in the ground colour and pattern. The conspicuous neck stripes of *Phelsuma andamanensis* are similarly pronounced in the types of the North Island form (*Phelsuma longinsulae rubra*) where they are part of the longitudinally fused rows of red blotches, and they may sometimes be seen in other Seychelles specimens as well. The back pattern of *Phelsuma andamanensis* (except the neck stripes) is very similar

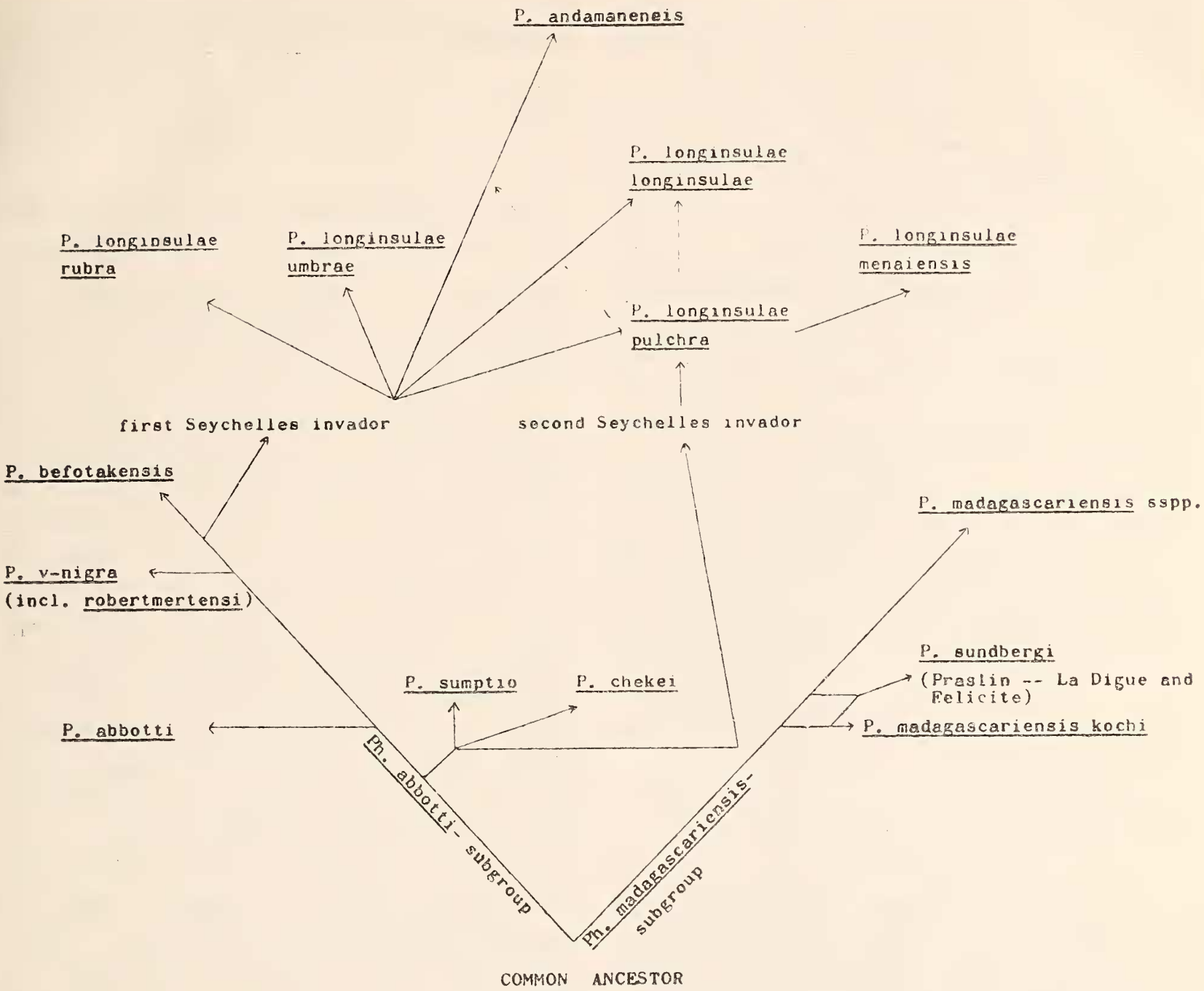


Fig. 2. Phylogenetic tree.

to that of the Silhouette form. The facts that in contrast to these Seychelles forms *Phelsuma andamanensis* has a more yellowish vent, contains concolorous specimens and has no reduced number of preanal pores, may be explained by the long isolation of *Phelsuma andamanensis*: It originated from an ancestor of the Seychelles forms of nowadays, and it underwent a separate evolution in a closed gene-pool during its isolation on the Andaman Islands.

Phelsuma chekei has a shorter tail, a stouter, more robust shape, a shorter fore head, and a coarser scutellation (except the gulars) than *Phelsuma andamanensis*. Furthermore, *Phelsuma chekei* differs by its prominent blue factor in colour and pattern and its different chin and lateral head pattern. *Phelsuma chekei* is a more reeent invader of the Indian Ocean; before it spread to the Seychelles it would have had to travel more than 5600 km NE from the north tip of Madagascar to the Andaman Is-